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Population Collapse of the Crayfish *Orconectes virilis* in Response to Experimental Whole-Lake Acidification

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Davies, I. J. 1989. Population collapse of the crayfish *Orconectes virilis* in response to experimental whole-lake acidification. Can. J. Fish. Aquat. Sci. 46: 910–922.

A population of *Orconectes virilis* in Lake 223 at the Experimental Lakes Area, northwestern Ontario, was monitored from 1976 to 1982 during an acidification experiment. *O. virilis* from nearby Lake 240 served as a reference population. Crayfish abundance remained stable as average epilimnion pH was gradually lowered from 6.49 (1976) to 5.93 (1978). In 1979 (pH 5.64) recruitment of young was poor and the overall population size ($\bar{X}$) fell from 105 800 to 60 300 animals. The decline continued in the complete absence of recruitment during 1980 (pH 5.59, $\bar{X}$ = 32 000) and 1981 (pH 5.02, $\bar{X}$ = 8000). Few crayfish survived until the spring of 1982. None were present from mid-summer 1982 to fall 1983 (average pH 5.09 to 5.13). Hatchling mortality and some egg loss appeared to have been the causes of recruitment failure. Acidification also produced a noticeable softening in the carapace of all intermoult crayfish. Growth, mortality, behaviour, and the basic reproductive functions of juvenile and adult crayfish did not change in response to acidification. Fish predation and the incidence of a microsporidian parasite apparently contributed little to the population decline.

De 1976 à 1982, au cours d'une expérience sur l'acidification, on a suivi l'évolution d'une population d'*Orconectes virilis* habitant le lac 223 dans la Région des lacs expérimentaux située dans la partie nord-ouest de l'Ontario. La population d'*O. virilis* se trouvant à proximité dans le lac 240 a servi de témoin. Le nombre d'écrevisses est demeuré stable à mesure qu'on a abaissé graduellement le pH moyen dans l'épilimnion de 6,49 (1976) à 5,93 (1978). EN 1979 (pH de 5,64) le recrutement des jeunes a été faible et la taille de la population globale ($\bar{X}$) a diminuée, passant de 105 800 à 60 300 individus. Cette baisse s'est poursuivie en l'absence totale de recrutement au cours de 1980 (pH de 5,59; $\bar{X}$ = 32 000) et de 1981 (pH de 5,02; $\bar{X}$ = 8000). Peu d'écrevisses ont survécu jusqu'au printemps de 1982. On n'en a trouvé aucune du milieu de l'été 1982 à l'automne de 1983 (pH moyen variant de 5,09 à 5,13). La mortalité des individus récemment éclos et une certaine perte d'oeufs ont semblé être les causes de l'échec observé du recrutement. L'acidification a provoqué également un ramollissement perceptible de la carapace chez toutes les écrevisses se trouvant entre deux mues. La croissance, la mortalité, le comportement et les fonctions reproductrices de base des écrevisses jeunes et adultes n'ont pas changé par suite de l'acidification. La prédation par les poissons et l'apparition d'un parasite de la classe des microsporidies ont été, semble-t-il, peu responsables de la baisse de la population.

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The occurrence of waters low in pH and calcium restricts the distribution of molluscs and some crustacean species in Finland, Scandanavia, and Germany (Wiederholm and Eriksson 1977; Nilssen 1980; Økland and Økland 1980), as well as in parts of Great Britain (Jones 1948; Macan 1950; Sutcliffe and Carrick 1973; Fryer 1980; Jay and Holdich 1981). North American surveys suggest that a similar pH–calcium interaction controls the distribution of molluscs and crustaceans among softwater lakes on the Canadian Precambrian Shield (McKillop and Harrison 1972; Roff and Kwiatkowski 1977; Berrill et al. 1985; Stephenson and Mackie 1986). European authors have proposed that the natural ranges of some taxa have been narrowed over the last few decades by the widespread influence of acidic precipitation, but such claims are largely based on synoptic, rather than direct evidence. The abundance of invertebrate species has only been measured in a few cases over the course of a lake acidification process (Allison and Harvey 1981; Nero and Schindler 1983).

In 1976, an 8-yr whole-lake acidification programme was undertaken in Lake 223 (L223) at the Experimental Lakes Area (ELA), northwestern Ontario to examine the chemical and biological consequences of lake acidification (Schindler 1980; Schindler et al. 1980; Schindler et al. 1985). Prior to acidification, the lake supported a population of the crayfish *Orconectes virilis*. The genus *Orconectes* contains several species that are widely distributed throughout the acid-sensitive softwater lakes of eastern and central Canada (Crocker and Barr 1968; Berrill 1978) and parts of the northern United States (Capelli 1975), but is only represented by *O. virilis* at ELA. Although crayfish were numerous in L223, there was some indication that conditions for their growth were suboptimal. Preacidification values of dissolved calcium ($\approx 2\ mg \cdot L^{-1}$) were below the environmental tolerance limits for crayfish suggested by Capelli (1975). For both maximum length and size at the onset of sexual maturity, crayfish from L223 were smaller by 1.0–1.5 mm of carapace length than their counterparts in nearby lakes. The largest *O. virilis* from L223 were also smaller than representatives of the same species from other locations (Threinen 1958; Aiken 1967; Weagle and Ozburn 1972; Capelli 1975;

Momot 1978; France 1985). Thus, it seemed likely that the crayfish in L223 would succumb to the effects of acidification both because they appeared to be living at the limits of their environmental tolerance and because *O. virilis* has been shown to be among the least tolerant of crayfish species to conditions of low pH and low calcium (Capelli 1975; Malley 1980; Berrill et al. 1985).

In anticipation of this result, the abundance, population dynamics, and the condition of crayfish in L223 were monitored over the course of the experiment. Later a reference population of *O. virilis* in a nearby untreated lake (L240) was monitored from 1981 to 1985 to confirm that changes seen in the L223 study lay beyond the expected limits of natural variability.

Methods

Characteristics of the Study Lakes

Lake 223 is an oligotrophic, soft water, dimictic lake, 27.27 ha in surface area, with a maximum depth of 13.5 m. From 1976 to 1984, the lake was acidified by frequent additions of H_2SO_4 to gradually lower its pH to a minimum target value of 5.0 by 1981. Annual values of epilimnetic pH reported here were calculated from time weighted means of H^+ concentration. Whole-lake values contain an additional volume correction. Chemical data is from Cruikshank (1984) and from M. A. Turner (Freshwater Institute, Winnipeg, Man., pers. comm.). Details of lake morphometry and the experiment are given in Schindler (1980); Schindler et al. (1980); Schindler and Turner (1982); and Cruikshank (1984).

Lake 240, the nearby reference system, is an oligotrophic, dimictic lake with a surface area of 26.7 ha and a maximum depth of 13.1 m. Lake morphometry is given in Brunskill and Schindler (1971). Epilimnion pH ranged from 6.8 to 7.0 and Ca^{2+} concentrations were 2–3 $mg \cdot L^{-1}$.

Habital Surveys and Mapping

SCUBA divers observed that crayfish remained hidden throughout the day, but left their retreats after dark to forage on the substrate. Most animals showed little reaction to divers or underwater lights at night. Crayfish abundance was greatest in areas which afforded good cover such as boulder, cobble, or coarse gravel substrates. There was little emergent vegetation around the shores of L223 or L240 to provide additional refuge. Crayfish were rarely seen on the sandy bottom at the north end of L223 or on the loose flocculent sediment below the maximum depth of the summer thermocline in the central basin and at depths greater than 6 m in the outflow bay.

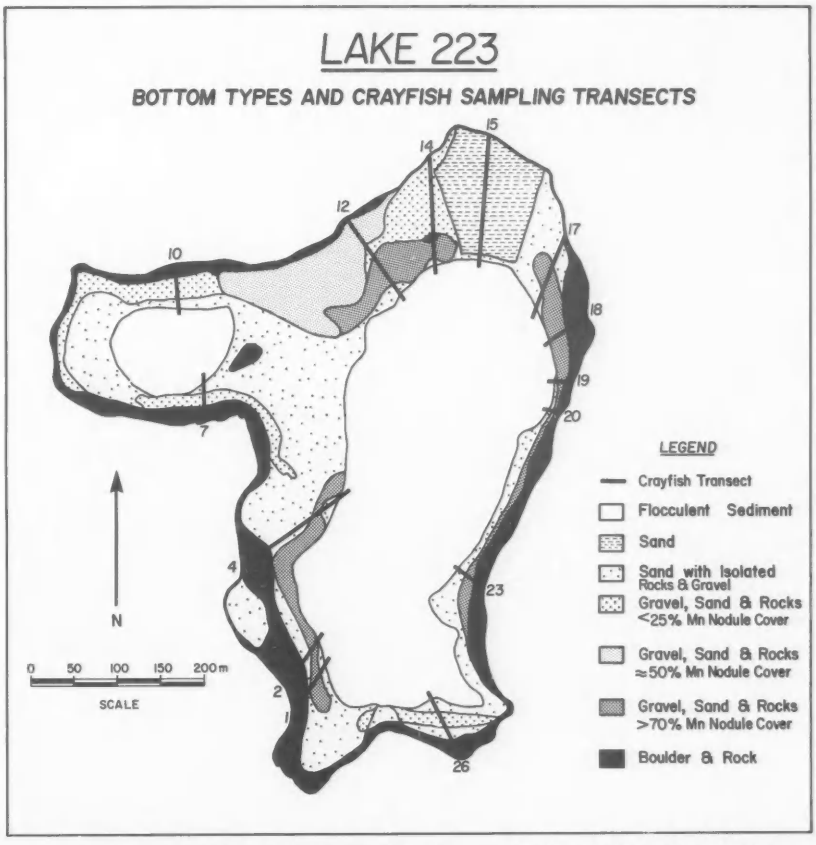

FIG. 1. Bottom types in L223 as determined by SCUBA survey. Darkest shading indicates habitat most favoured by crayfish; lighter shading, less preferred substrates. The location of census and sample collection transects are shown as solid lines.

To estimate the amount of usable crayfish habitat, SCUBA divers conducted a survey of L223 bottom type. Surface attendants in radio contact with divers plotted location and habitat information on bathymetric maps. A composite of these data is shown in Fig. 1. Depth stratified estimates of the total area occupied by each habitat type were calculated by digitizing the map. Overall accuracy of the technique is estimated to be ±20%.

Population Census

SCUBA divers determined the annual abundance of crayfish in L223 by counting the number of animals present along 1-m wide transects at night. Transect ropes, installed along the substrate between shore and a point several metres beyond the flocculent sediment boundary at each of several locations around the lake (Fig. 1), were divided into several intervals of depth. These segments were further classified by bottom type. Transect sampling was chosen in preference to doing a survey of random plots, to simplify the job of locating sample stations at night. Although crayfish distribution was highly dependent on depth and habitat type, it appeared to be independent of crayfish abundance in adjacent areas, so samples were treated as if they were random. Survey data, segregated by depth and by habitat type, were used in a stratified random sampling model (Sampford 1962; Snedecor and Cochran 1967) to construct whole-lake crayfish population estimates.

Habitat classifications were as follows: (1) areas without crayfish; bare sand or flocculent sediment, (2) areas with limited or poor crayfish refuge; gravels or sand with up to 25% cover, and (3) good habitat; those areas with more than 25% cover.

For the 1976 survey, eight transects were marked in 3-m depth intervals and the horizontal length of each interval was recorded. Divers, using a 1-m long rod to define the width of the survey strip, counted the entire length of each transect at night. Starting in 1977, 10-m^2 transect sections and 2-m depth intervals per stratum were used to equalize sampling effort among strata and obtain greater sampling precision. On steep sections of shore where there was <10 m of transect length per depth interval, 10-m long lateral lines, placed perpendicular to the main transect, were counted instead. Population surveys were done each fall from 1976 to 1981 and in the spring of 1981, along an average of eight (range 7–10) transects. In August 1984, five transects were counted. Changes in the survey locations were made only to overcome sampling difficulties. Additional qualitative surveys of large areas of lake bottom were done by divers between 1982 and 1984 to confirm the absence of crayfish in these years.

Depth-stratified estimates of crayfish abundance were also done each fall from 1981 to 1984 in the reference lake (L240). Using the census technique developed for L223, divers counted crayfish along two transects set perpendicular to the south shore of the island in L240.

Crayfish Collections

Animals were collected in the spring and fall of each year (and more frequently in 1977 and 1981) to help evaluate changes in the size/age structure of the crayfish population and the general condition of individuals. Following an initial period of testing, baited wire traps were rejected as a means of sampling crayfish because of an apparent size and sex bias associated with trapping (Capelli 1975, 1982; Davies and Ramsey 1989). Instead, divers made collections in the vicinity of transects 2 and 18 (Fig. 1) at night by using a suction gun and self-closing sample container (Davies and Ramsey 1989). However, even with the gun technique, young-of-the-year *O. virilis* were poorly represented in the collections from all years, not because they were small or difficult to capture, but because they tended to remain hidden from view in the substrate (Capelli 1975; Stein and Magnusson 1976; Stein 1977).

Divers made a conscious effort to avoid size bias by attempting to capture all animals seen. More than 90% of all capture attempts were successful. Collecting was stratified by depth in intervals of 3 m and limited to 20–30 min per stratum so that relative abundance of crayfish (catch per unit effort) and the depth distribution of the population could be calculated. With the possible exception of collections made in 1981, ≤2% and usually <<1% of the estimated population of crayfish was removed annually. SCUBA surveys confirmed that any local depletion of animals was quickly made up by immigration from adjacent areas.

Crayfish Measurements

Live specimens were transported back to the laboratory where they were sorted by size and reproductive condition into several holding tanks to minimize damage from conspecifics during agressive interactions. Animals were usually processed within 24 h of capture.

Total length, measured from the tip of the acumen to the posterior margin of the telson, excluding the hair fringe, was used to characterize the size of individuals in 1976. Beginning in 1977, measurements of dorsal carapace length (tip of the acumen to the posterior margin of the cephalothorax, ±0.05 mm) and wet weight (excess water removed by blotting animals with damp toweling, ±0.01 g) were included. After 1978, measurement of total length was discontinued and 1976 values of total length (T) were converted to carapace length (C) by using the regression relationship:

$$C = 0.493T - 0.913 \; (N = 858, r^2 = 0.98)$$

derived from 1977–78 data.

Crayfish were examined for exoskeleton damage and missing, broken or partially regenerated limbs. In 1979, a characteristic cream-coloured opacity of the muscle tissue, indicative of parasitism by the microsporidian *Thelohania contejeani* was noted for the first time in L223 crayfish and later confirmed by France and Graham (1985). Beginning in spring 1980, the number of infected individuals in each collection was noted.

To determine whether or not lake acidification had interfered with the calcium metabolism of *O. virilis* (Malley 1980), carapace rigidity of each specimen was tested by squeezing the sides of the cephalothorax between the thumb and forefinger. Sample collection periods were usually chosen to coincide with times of the year when most crayfish were in the intermoult stage (Stevenson 1975) and had achieved the maximum degree of exoskeleton hardening by calcification. Intermoult crayfish from L240 served as a calibration reference for the squeeze test. Hardness was scaled in five degrees from gelatinous, to very flexible, moderately flexible, slightly flexible, or inflexible. Average population hardness was calculated as a weighted mean by assigning these operational definitions of flexibility, values of 0, 25, 50, 75, and 100% of maximum hardness, respectively.

The sex and reproductive state of each specimen was noted and categorized as follows: sexually active (form I) male, sexually inactive (form II male), sexually active female (indicated

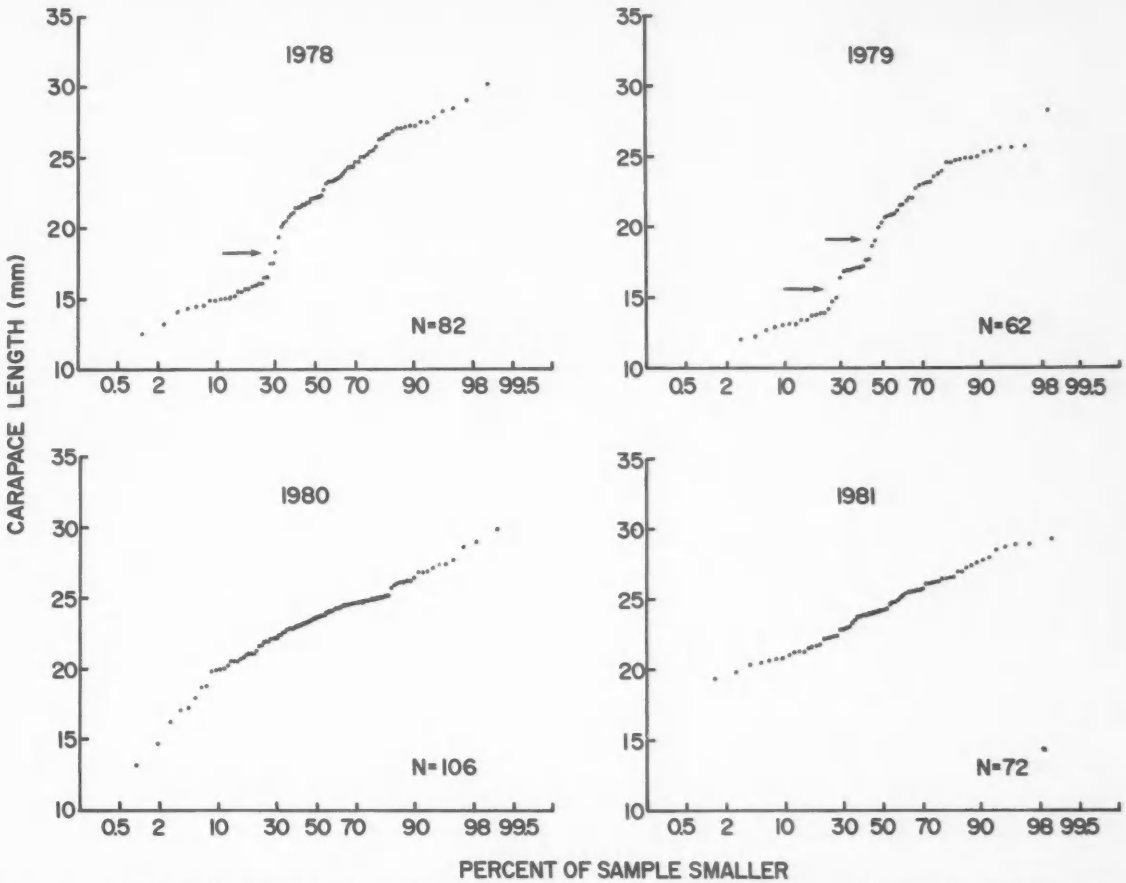

FIG. 2. Probability plots of length-frequency for male *Orconectes virilis* samples each spring prior to the period of moulting from 1978 to 1981. For any length (y axis), values on the x axis give the percentage of the total sample (*N*) that was equal to or less than that carapace length. Arrows mark the mid point of vertical discontinuties in the curves which correspond to upper length limits of distinct size classes.

by the presence of developed abdominal cement glands), berried female (carrying eggs — data not recorded from 1976 and 1977 collections), and sexually inactive female. Berried female crayfish were examined to determine total pleopod egg count, the number of dead or fungus infected eggs and the development stage of healthy eggs. The presence of empty egg capsules on the pleopods of these individuals was taken as evidence of egg loss. Because it was difficult to obtain an accurate count of egg capsules from an in vivo examination, their numbers were noted categorically. Thus, egg loss was recorded as: none, slight (1–5), moderate (5–10), severe (>10), or complete based on the number of empty egg capsules found.

In 1982, a berried female captured from L223 was held in an aquarium containing nonacidified lake water until the eggs hatched, to test whether or not long term exposure to the acidic conditions of L223 had diminished the inherent reproductive capacity of *O. virilis*.

Analysis of Sample Collection Data

Life history

Data and observations from the periodic collection of crayfish were used in conjunction with information reported by Weagle and Ozburn (1972) to develop a basic scheme for the life history of *O. virilis* in L223 and L240. Catch per unit effort (number caught per minute) and the relative abundance of male and female *O. virilis* in the sample collections were used to document the dynamics of seasonal shifts in depth distribution of the population.

Population size structure and growth

Hopkins (1967); Jones (1981); and Brewis and Bowler (1982) have shown that, although commonly applied, the technique of determining size or age structure of a population from ranked plots of length-frequency data on normal probability paper (Harding 1949; Cassie 1954) is of limited use when size classes are closely spaced and overlap broadly. Such was the case with both male and female components of the adult *O. virilis* populations in L223 and L240. Even though collections were made in the spring or fall when few individuals were moulting, it was not possible to distinguish among cohorts older than age 1+ on the basis of carapace length (Fig. 2) or total wet weight. However, young-of-the-year and juvenile crayfish formed distinct size classes that were easily recognizable, though not always present in the collections (Fig. 2, 1980, 1981).

As an alternative to cohort analysis, size-frequency histograms were constructed to demonstrate a progressive shift in population size structure. Probability plots were used to assign both interval width and the boundary between the first and second length classes such that the first bar of each histogram represented the relative abundance of young at the end of their first summer season (age 0+), whereas the second bar represented juveniles age 1 in the summer and 1+ in the fall. The remaining four divisions were simply multiples of the initial interval width and only loosely reflected age.

Patterns of *O. virilis* growth were examined for evidence of change due to acidification. Both the frequency of moulting and the relationship between carapace length and specimen wet weight, calculated as a simple linear regression on ln transformed data, were compared among years of the experiment.

Reproduction and mortality

To evaluate the effects of acidification on the reproductive potential of *O. virilis*, spring collections were used to estimate the size of the breeding population, potential fecundity, egg loss, and egg mortality. Size of the smallest, sexually mature individuals in the periodic collections was used to define the division between juveniles and adults. For L223, males ≥21.05 mm or females ≥19.16 mm carapace length were classified as adult based on data from the preresponse years (1976–78). For L240, carapace lengths of ≥21.55 mm for males or ≥21.05 mm for females (1981–84 data) were chosen to represent adult size.

Reductions in reproductive potential due to egg loss were estimated for *O. virilis* from L223 (1979–81) and from L240 (1984–85). In the absence of quantitative data on the abundance of empty egg capsules, egg loss was calculated empirically. Theoretical egg count for adult females in each spring collection was determined from first-order regression relationships between carapace length and egg count for berried females showing no evidence of egg loss. Regression calculations were based on 1978–79 combined data for L223 and data for the year of each collection in reference L240. The difference between this theoretical value and the actual egg count was called "egg loss."

Mortality could not be estimated by the conventional techniques outlined by Ricker (1975) without prior knowledge of population age structure. Because it proved impossible to use length-frequency analysis to distinguish among age classes in the L223 or L240 populations, the impact of acidification on juvenile and adult mortality could not be determined directly. However, it was possible, by means of a conceptual model of population dynamics, to derive a theoretical age structure for the *O. virilis* population present in 1978 (i.e. preimpact) and from this, generate estimates of mortality for comparison with typical values for the species that have been reported in the literature.

In the absence of recruitment, the loss of crayfish from year-to-year could be attributed to death of the oldest individuals plus the sum of annual mortality in all the other cohorts. Each year, one less cohort remained until in 1982 when, after four successive years of recruitment failure, the population became extinct. Thus, in the fall of 1981 the entire population had consisted of individuals aged 3+. In 1980, individuals aged 2+ and 3+ were present. The difference between the 1980 and 1981 estimates of total crayfish abundance, therefore, represented the number of individuals aged 2+ that were present in the fall of 1980. By continuing to trace the process backwards in time, it was possible to estimate the number of crayfish present in each age class in the fall of 1978, the last year in which all cohorts were present. Actual population totals, size, and sex composition data (1977–79 combined data) were used to estimate that in the spring of 1978 18 000 females of average carapace length 22.5 mm were carrying eggs. Total egg count was calculated from the regression relationship: egg count = $-165.44 + 10.05 \times$ carapace length ($r^2 = 0.650$, $N = 22$, 1978–79 combined data). Once the population structure was established age-dependent mortality was calculated for 1978 from the relative abundance of successive cohorts. An underlying assumption of the model was that patterns of mortality did not change during the course of the population collapse. The validity of this assumption and the consequences of any errors in it are examined in the next section.

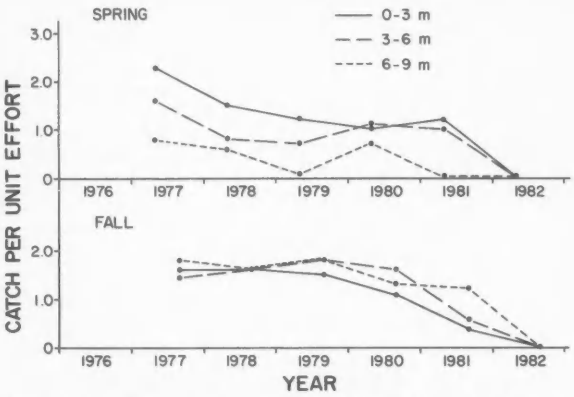

FIG. 3. Average number of crayfish caught per minute by divers in three depth strata sampled in the spring (upper panel) and fall (lower panel) each year of the L223 experiment.

Results and Discussion

Life History of *O. virilis*

Based on information from the periodic collections and miscellaneous diver observations in L223 (1976–82) and L240 (1981–85), the life history of *O. virilis* in both lakes appeared to follow the scheme proposed by Weagle and Ozburn (1972), except that most adult males and nonovigerous females moulted twice, rather than once, annually. Adult crayfish overwintered in the sexually active form. When epilimnion temperature rose above 10°C in middle to late May, females extruded eggs and began to carry them. Adult males, nonovigerous females, and juveniles began to moult to the sexually inactive form late in May. The peak of spring moulting activity was not reached until late June, coincident with the time of egg hatching. A major moulting period for the whole population began early in August. For juveniles, this corresponded to their second or third moult of the season; for adult males and females without eggs that year, their second; and for recently berried females, their first. Adults moulted to the sexually active form in August. An annual period of mating followed, and continued until freezeup, when most crayfish sought refuge for a period of winter torpor. Each fall a few animals, aged 1+, attained sexual maturity, although most remained as juveniles until the following year. Acidification of L223 did not change these basic patterns of crayfish life history.

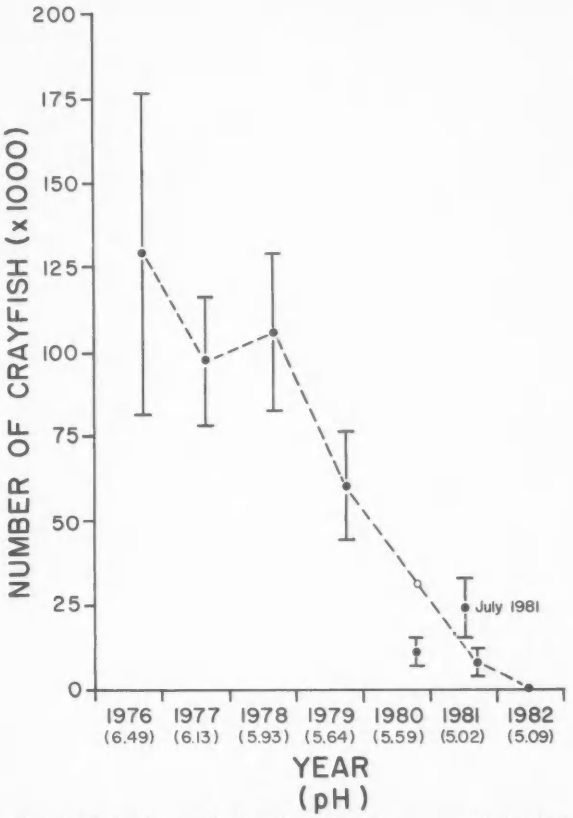

FIG. 4. Whole-lake population estimates for *Orconectes virilis* in L223 based on stratified areal census by SCUBA divers at night along transects. Surveys were done each fall and in the summer of 1981. Points represent means, bars are 95% confidence limits, numbers in parentheses are time weighted epilimnion pH values for the ice free season. An estimate of 32 000 crayfish present in the fall of 1980 (open circle) was derived by linear interpolation (see results and discussion).

Seasonal Distribution of *O. virilis* in L223

Although an annual movement of crayfish from shallow to deeper water has been observed in several systems, migration patterns appear to vary considerably. For *O. virilis*, Momot and Gowing (1972) reported a differential migration of the sexes to deeper waters. In contrast, Capelli (1975) noted an apparently synchronous downward extension of the summer range for both sexes in Trout Lake, Wisconsin.

Plots of catch per unit effort, segregated by depth for annual spring and fall collections (Fig. 3) showed the seasonal pattern of crayfish depth redistribution in L223. In the spring and early part of the summer, few individuals were found below the 4–5 m thermocline depth, but in July, when the thermocline began to deepen, the lower boundary of the population moved downward to include areas of suitable habitat within the upper portions of the hypolimnion. No evidence of any differential seasonal movement of the sexes could be found in the L223 study. By late fall, adults, juveniles, and young-of-the-year (when present in the population) were seen at all depths. The ecological reasons for this annual depth redistribution are not known. However, it is possible that during the sexually inactive part of the life cycle (summer) individuals seek greater spacing to minimize aggression (Bovbjerg 1956; Abrahamsson 1966; Momot 1967; Momot and Gowing 1972) or to maximize food availability.

Declines in catch per unit effort in the final years of the population collapse (Fig. 3) reflected a major decrease in crayfish abundance. The relatively stable values from 1977 to 1980 resulted from the fact that divers were physically unable to capture more than two or three specimens per minute, even when crayfish were very abundant. Higher than average values of catch per unit effort in the spring of 1977 were likely the result of inaccuracies in timekeeping during the first trials of the stratified collection method.

In the fall of 1981, few crayfish were found at the two shallowest depths (Fig. 3). Despite an overall reduction in the size of the population, the relative abundance of *O. virilis* in the deepest stratum remained similar to the 1980 value. This result suggested that in 1981, during the most severe phase of the acidification (pH 5.02), a higher than normal proportion of crayfish moved into the comparatively well-buffered hypolimnion which had consistently remained between three-quarters and one pH unit higher than the epilimnion that summer (Linsey and Braund 1984). It is not clear, however, whether this migration was based on active avoidance of low pH waters or was related to other factors.

Changes in Population Size and Structure

Results of the diver-based population surveys, outlining the decline of *O. virilis* in L223 are shown in Fig. 4, along with mean values of epilimnetic pH for the open-water period each year. During the first 3 yr of monitoring, L223 had a stable population of approximately 100 000 crayfish. A high level of uncertainty surrounded the 1976 estimate of population size (129 000 ± 47 500, 95% confidence limits). However, when the transect stratification scheme was modified the following year, precision of the estimates for 1977 (97 400 ± 18 900) and subsequent years was greatly improved. By 1979, mean annual lake pH had reached 5.63 and mean epilimnetic pH was 5.64 for the open-water period. That fall, the population abundance of *O. virilis* (60 300 ± 16 000) was 43.0% lower than the previous year (1978 estimate: 105 800 ± 23 000). Young-of-the-year were rarely seen. The population decline continued during 1980 when epilimnion pH was further lowered to an average value of 5.59.

France (1985) reported that young-of-the-year crayfish were present in L223 in 1980, but divers making collections for this study did not see any young during a 2-h search on 20 September 1980. The absence of young from the collections raised two possibilities: either few or no young were present in the lake, or acidification had retarded their growth and these smaller crayfish continued their normal pattern of behaviour and remained hidden from view. To accommodate this second possibility, the usual mid-September population survey was delayed until October 1980 to allow more time for young to complete their first season's growth and thus enhance the divers' chances of seeing them. A population estimate of 11 000 ± 4300 animals resulted from the delayed census (Fig. 4). Contrary to expectations, young were not seen. Overall, crayfish abundance was also noticeably lower than it had been 2 wk earlier (20 September) when the collections were made, suggesting that in the interim many crayfish had either sought winter refuge and become torpid, or had died.

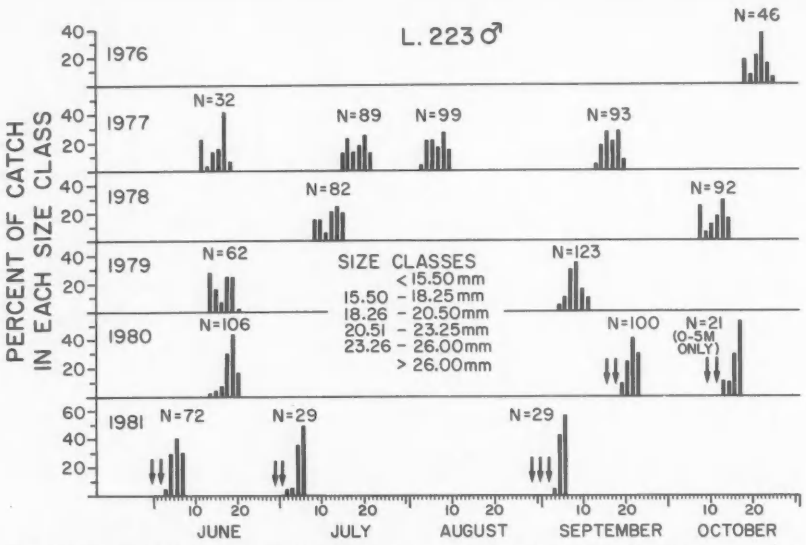

FIG. 5. Size structure of the male population of *Orconectes virilis* in L223 based on periodic diver collections. Rows represent separate years. Groups of six bars form length-frequency histograms for each catch and are centered on the sampling dates. Vertical arrows indicate size classes not represented in a collection. *N* denotes the number of males in each catch.

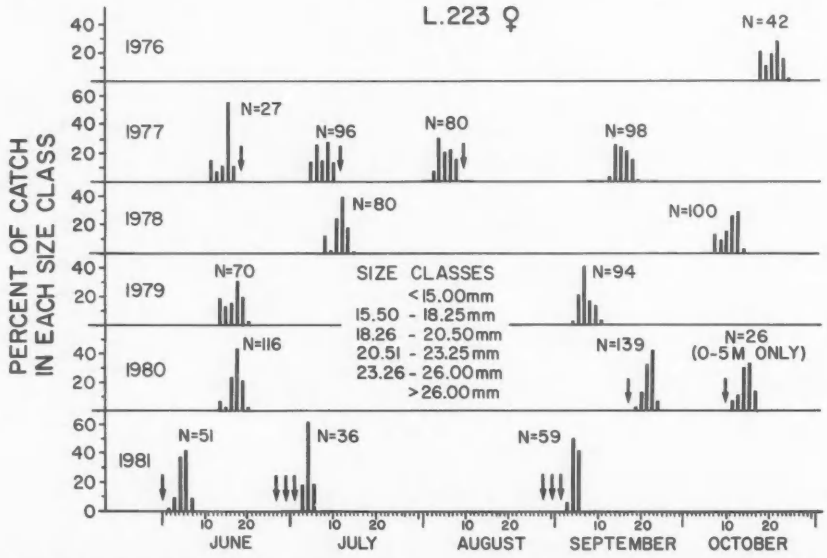

FIG. 6. Size structure of the female population of *Orconectes virilis* in L223 based on periodic diver collections. Rows represent separate years. Groups of six bars form length-frequency histograms for each catch and are centered on the sampling dates. Vertical arrows indicate size classes not represented in a collection. *N* denotes the number of females in each catch.

The survey was redone 7–14 July 1981 and yielded a population estimate of 24 200 ± 8000 (Fig. 4). Although this result confirmed the suspicion that many animals had been missed in the previous fall survey, it could not be used to estimate the standing stock of crayfish present in October 1980 because overwinter mortality had acted to reduce the standing stock by some unknown amount during the intervening months. Instead, crayfish abundance during the fall of 1980 was estimated to be 32 000 individuals, by linear interpolation between the fall 1979 and fall 1981 data points (Fig. 4).

By mid-September 1981, the total number of crayfish had fallen to 8000 ± 4200. Again, no young were seen. A few large crayfish survived until the following spring, but by mid-summer 1982 these too had disappeared. A 1.5-h search in the spring of 1983 along several survey transects and in other parts of the lake and a transect survey in mid-summer of 1984, both

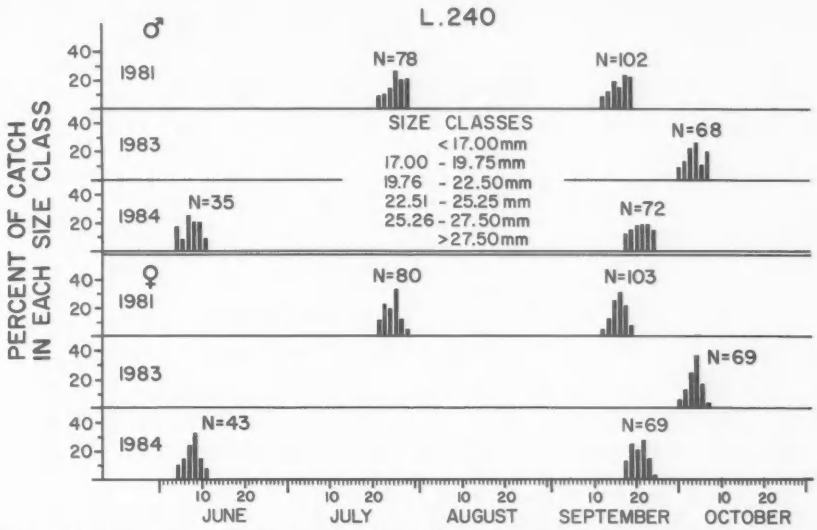

FIG. 7. Size structure of the male (upper panel) and female (lower panel) populations of *Orconectes virilis* in reference L240 based on periodic diver collections. Rows represent separate years. Groups of six bars form length-frequency histograms for each catch and are centered on the sampling dates. *N* denotes the number of male or female specimens in each sample.

confirmed that crayfish were absent from the lake. By comparison, in L240, crayfish population density (0.62–0.74 individuals·m^{-2}) remained relatively constant from 1981 to 1984 and showed good recruitment of young in each year.

Loss of crayfish from an acidified system has only been documented in one other case. Allison and Harvey (1981), using the census technique developed for the L223 study, recorded a 1-yr reduction in crayfish abundance of 68% in Crosson Lake, Ontario. Prior to the decline, the lake contained three species of crayfish (H.H. Harvey, University of Toronto, pers. comm.). *Orconectes virilis*, the most acid sensitive of the three (Berrill et al. 1985), made up the largest fraction (≈80%) of the total population but *O. propinquuis* and *Cambarus bartoni* were also present. Although species composition data were not available for the period following the decline, the magnitude of the change and the known sensitivity of the species suggests that the *O. virilis* population was severely affected by the Crosson Lake acidification.

As the abundance of *O. virilis* declined in L223 (1979–82), the size structure of the population became progressively altered due to repeated recruitment failures. Data illustrating this shift in size structure (Fig. 5 and 6) were derived from the periodic diver collections of crayfish from L223. The size structure of an *O. virilis* population from untreated L240 is given in Fig. 7 for comparison. Although there was little temporal overlap between the sampling programs in the two lakes, results from L240 closely matched those from the preeffect years (1976–78) of the L223 experiment and were therefore assumed to be typical of stable crayfish populations.

Except for samples taken in October, young-of-the-year (shown as the first bar in each histogram) were consistently undersampled and thus poorly represented in the early fall collections. A strong presence of this same length class in collections made the next spring (i.e. age 1 individuals) was taken as evidence of successful recruitment in the previous year.

Between 1976 and 1978, recruitment of young appeared normal for the L223 population (Fig. 5 and 6). Spring collections in 1980 showed a much reduced complement of animals in the lower two size classes for both males and females suggesting that a major, though not total, recruitment failure had occurred in 1979 (lake average pH = 5.64). The absence of young-of-the-year from both early and late fall collections in 1980 suggested that a second recruitment failure had occurred that year. Total recruitment failure in 1980 was confirmed by the absence of age 1 individuals from collections made in the spring of 1981. A third consecutive year-class failure followed in the summer of 1981, leaving only a remnant of the former population by early fall. The only individuals captured (N = 15) in June 1982 during a 2.5-h search by divers were males and females of the largest size class. No crayfish were found after this date. By comparison, the size structure of the *O. virilis* population in L240 remained stable from 1981 to 1984 (Fig. 7).

These results indicated that in soft waters of L223 chronic exposure of *O. virilis* to pH ≤5.64 led to recruitment failures and eventually to extinction. Several mechanisms may have acted to produce this result. Recruitment failure may have been caused by loss of fertility, egg loss or egg mortality during incubation, or the death of hatchlings. In addition, a change of growth or the condition of juveniles and adults may have weakened these individuals and made them more susceptible to natural or disease-induced mortality. Data from the periodic sample collections (summarized in Table 1) together with the results from the published literature were used to evaluate each of these potential mechanisms of population failure.

Reproduction and Hatchling Mortality

Patterns of mating and egg laying continued normally throughout the course of the L223 experiment, but because females carried eggs for only a short time each year, the percentages of berried females in the collections (Table 1) were

TABLE 1. Temporal summary of population characteristics of *O. virilis* in L223 and reference L
on the collection dates noted. Dashes indicate categories for which no data were recorded or ca

		Lake mean		Total ♂ + ♀				
Lake and date	Year	Epilimnion pH	Ca^{2+} ($mg \cdot L^{-1}$)	*N*	Percent ♂	Percent *Thelohania* infected	Percent damaged	Hardness as percent of maximum
Lake 223								
13 and 20 Oct.	1976	6.49	2.55	88	52.3	—	—	—
12 and 14 Jun.	1977			59	54.2	—	6.8	70.8
4 and 10 Jul.	1977	6.13	2.65	185	48.1	—	7.6	50.1
2 and 9 Aug.	1977			178	55.6	—	6.2	50.8
12 and 19 Sep.	1977			191	48.7	—	6.8	66.6
23 Jun., 10 and 11 Jul.	1978	5.93	2.60	162	50.6	—	8.6	47.2
8 and 10 Oct.	1978			192	47.9	—	7.3	79.0
6, 12 and 21 Jun.	1979	5.64	2.63	132	47.0	—	6.1	73.5
5 and 6 Sep.	1979			217	56.7	—	4.6	47.5
11, 12, and 18 Jun.	1980			222	47.8	—	5.9	36.6
19 and 20 Sep.	1980	5.59	2.63	239	41.8	5.4	5.9	45.5
14 Oct (0.5 m)	1980			47	44.7	6.4	10.6	60.6
2 and 3 Jun.	1981			123	58.5	5.3	10.6	54.5
1 Jul.	1981	5.02	2.82	65	44.6	0.1	10.8	40.0
31 Aug. and 1 Sep.	1981			88	33.0	4.6	11.4	25.6
21 Jun.	1982	5.09		15	33.3	0.0	40.0	30.0
Lake 240								
28 Jul. and 3 Aug.	1981	6.80†	2.43[a]	297	55.2	0.3	5.7	63.0
16 Sep.	1981			204	50.0	2.9	4.4	89.9
11 Aug.	1982	6.86	2.50[b]	139	44.6	0.7	5.0	56.3
4 and 5 Oct.	1983	6.96	2.34[b]	137	49.6	0.0	2.9	73.4
7 Jun.	1984	6.79	2.62[b]	78	44.9	0.0	6.4	62.5
21 Sept.	1984			141	51.1	1.4	2.1	70.6
3 Jun.	1985	6.76	2.59[b]	44	56.8	9.1	—	—
11 Jun.	1985			93	52.7	10.8	6.5	39.7

[a]Open water means for outflow.
[b]Open water means for epilimnion.

rence L240. Data were derived from measurements on specimens gathered by SCUBA divers at night
ed or calculated.

	Total ♂	Adult ♂	Total ♀	Adult ♀			Wet weight (g) versus carapace length (mm)		
rdness percent aximum	Percent as adult	Percent sexually active	Percent as adult	Percent berried	Percent of berried ♀ with egg loss	Percent egg reduction	Equation	*df*	r^2
—	54.3	—	52.4	—	8	—	—	—	—
70.8	56.2	88.8	74.1	—	—	—	$W = 1.152\ 10^{-4}\ L^{3.237}$	519	0.958
50.1	50.6	33.0	50.0	—	—	—			
50.8	52.5	82.7	43.0	—	—	—			
66.6	48.4	73.3	53.1	—	—	—			
47.2	63.4	34.6	71.2	14.0	—	—	$W = 6.302\ 10^{-5}\ L^{3.430}$	313	0.990
79.0	59.8	94.5	67.0	0.0	—	—			
73.5	43.5	77.7	58.6	87.8	34.8	28.3	$W = 9.073\ 10^{-5}\ L^{3.311}$	284	0.990
47.5	52.0	65.6	46.8	0.0	—	—			
36.6	83.0	5.7	83.5	37.5	33.3	20.9	$W = 7.278\ 10^{-5}\ L^{3.377}$	427	0.969
45.5	88.0	77.3	90.7	0.0	—	—			
60.6	90.5	78.9	84.6	0.0	—	—			
54.5	90.3	86.2	92.2	75.0	44.0	34.7	$W = 1.956\ 10^{-4}\ L^{3.068}$	215	0.936
40.0	93.1	0.0	100.0	38.9	100.0	68.3			
25.6	100.0	93.1	100.0	0.0	—	—			
30.0	100.0	60.0	100.0	90.0	—	66.8	—	—	—
63.0	40.7	71.9	62.4	2.1	—	—	$W = 6.736\ 10^{-5}\ L^{3.399}$	445	0.983
89.9	64.7	90.9	69.6	0.0	—	—			
56.3	46.2	58.3	56.3	0.0	—	—	$W = 8.816\ 10^{-5}\ L^{3.308}$	50	0.992
73.4	67.6	78.3	69.6	0.0	—	—	$W = 7.470\ 10^{-5}\ L^{3.324}$	131	0.988
62.5	60.0	85.7	65.1	78.6	59.1	15.8	$W = 9.072\ 10^{-5}\ L^{3.311}$	197	0.985
70.6	58.3	83.3	53.6	0.0					
—	—	—	—	—	50.0	2.8			
39.7	65.3	18.8	68.2	30.0	44.4	13.8	$W = 8.636\ 10^{-5}\ L^{3.307}$	87	0.980

highly variable, depending on when collections were made. For the L223 adult female population, maximum values of 87.8 and 75.0% berried individuals in the spring 1979 and 1981 collections, respectively compared favourably to a value of 78.6% for L240 females in 1984. Thus, sustained periods of exposure to acidified waters did not appear to affect the ability of female crayfish to produce viable eggs. Nor did it seem to affect the fertilization process. A berried female, captured from L223 in the spring of 1981 when lake pH reached 5.09, was held in circum-neutral water in the laboratory. All of the eggs she was carrying developed normally and hatched.

Occasionally, between 1979 and 1980, berried females from L223 were found carrying a few dead eggs mixed with larger numbers of apparently healthy ones. No females with dead eggs were found in L240. The percentage of dead eggs carried by L223 females in 1981 was only 0.9% (N = 48 females, 1836 eggs examined). France (1987b), in a separate study, reported levels of egg mortality for L223 of 0.4, 7.9, and 3.3% for 1979, 1980, and 1981, respectively, and hypothesized that egg mortality contributed to the population decline. The extent of this contribution would have probably been undetectable though, because natural mortality between the egg and young stages of development has widely been reported to equal or exceed 75% (Momot 1967; Momot and Gowing 1977; Momot 1978; France and Graham 1985). Thus, an 8% reduction in egg complement would result in <2% loss of recruitment.

Laboratory and field studies on other species have shown that crayfish eggs are relatively tolerant of acidic conditions. In acute toxicity tests, the eggs of *Astacus* sp. died only after they had been exposed to waters of pH ≤3.0 for >48 h (Appelberg 1983). The hatching success of *O. rusticus* and *O. propinquuis* eggs was severely reduced following a 20 d in situ exposure to waters in the pH range 4.1 to 4.8, but was largely unaffected at higher pH's (Berrill et al. 1985). Compared with other species of *Orconectes*, the eggs of *O. virilis* in L223 were slightly more sensitive to the effects of acidification. Although egg mortality did not appear to be the principal cause of recruitment failure, the presence of dead eggs served as a useful indicator of reproductive stress in the population.

Prior to hatching, eggs are secured to the pleopods of female crayfish by means of an elastic-like cement. Over the course of normal incubation, some of these eggs become dislodged and are lost. France (1987b) reported that in the late stages of the crayfish population decline the egg attachments became brittle and eggs could easily be removed. Appelberg (1984) also showed that significant egg loss occurred within 30 d of placing berried *Astacus* sp. females in pH 5.0 water.

Egg loss, calculated as the difference between the theoretical maximum and the actual egg count, was estimated to be between 20.9 and 34.7% for L223 crayfish (Table 1) during the period of the population collapse. A value of 68.3% loss (Table 1), recorded late in the 1981 incubation period, was excluded from the above range because it reflected both egg loss and a reduction in the egg complement due to hatching. These results agreed well with those of France (1987b) who estimated egg loss in L223 at between 18 and 31% for the same period by counting the number of empty egg capsules. The amount of loss attributable to acidification could not be determined because baseline data on egg loss were not recorded for L223 in the preimpact years. In 1979 and 1980, egg losses from female *O. virilis* in nonacidified reference lakes (including L240) were all low, averaging 3.2% (France 1987b). In subsequent years, losses were estimated to be 15.8% (1984) and

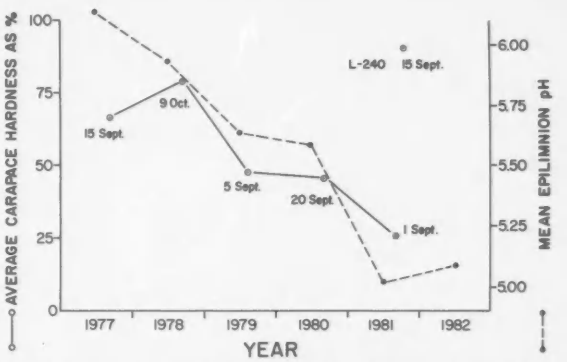

FIG. 8. Average decline of carapace rigidity of intermoult crayfish in L223 (solid line) and mean epilimnion pH (broken line) versus time. A single value for a fall 1981 collection in L240 is shown for comparison. Values for L240 animals collected in subsequent years are listed in Table 1.

13.8% (1985) in L240 (Table 1). The discrepancy between these two sets of results suggests either that loss rates were highly variable from year-to-year, or that the two methods of estimating egg loss gave different results in reference systems.

Regardless of the actual size of the difference, it appeared that egg loss in L223 from 1979 onward was considerably higher than in the reference lakes and may have contributed to the population decline in L223. However, since 75% to 95% mortality is considered normal for the egg to age 0+ stage of development (Momot 1967; Momot and Gowing 1977; Momot 1978; France and Graham 1985), the impact of this egg loss on recruitment was probably minimal. Indeed, it is probable that in the absence of other acidification effects, loss of eggs and the presence of fewer hatchlings would have acted to reduce density-dependent mortality in the young and maintain stable recruitment due to increased per capita food supply and lower probability of loss to predation.

Rather than a partial loss of young, the data showed a near complete recruitment failure in 1979 and no recruitment thereafter. This result suggests that young died after hatching when they were exposed to acidic waters. Experiments by Berrill et al. (1985) on two other species of *Orconectes (O. rusticus* and *O. propinquus*) showed that exposure to waters in the pH range 5.6 to 6.1 had little or no effect on egg or adult survival, but caused significant mortality among the hatchlings of each species.

A likely source of hatchling mortality was pH-related disruption of ionic regulation. Shaw (1960); Potts and Fryer (1979); Morgan and McMahon (1982); and Appelberg (1985) have demonstrated that low pH interferes with ionic regulation of Na^+ and Cl^- in crustaceans. Appelberg (1984) showed that at low pH, Na^+, K^+, and Ca^{2+} uptake rates were depressed in hatchling *Astacus astacus* and that hatchlings died when held at pH ≤5.5. The period of maximum ion loss in crayfish occurs during moulting. During ecdysis, stored calcium is remobilized and lost to the surrounding water. Sodium efflux is greatest just after the moult, indicating the high permeability of the new exoskeleton. Both Na^+ and Ca^{2+} are regained by active uptake from the water; little comes from the food (Bryan 1960). This pattern of ion loss, when coupled with inhibition of active ion-uptake by H^+, high moult frequency (5–7 moults in the first season) and their large surface to volume ratio, makes hatchlings the age group most likely to succumb to ionic stress.

Impact of Acidification on Juvenile and Adult Crayfish

Evidence to substantiate the claim that *O. virilis* experienced ionic stress at low pH came from measurements of carapace rigidity on animals that were periodically collected from L223 and L240. Minimum values of carapace rigidity occurred annually in both lakes during July and early August when most individuals were moulting (Table 1). Carapace hardness usually returned to near maximum values within a few weeks of a moult. Although acidification did not alter the timing of the moult cycle, the average value of *O. virilis* carapace rigidity in the fall declined steadily as L223 became more acidic (Fig. 8). France (1987a) showed that carapace rigidity in *O. virilis* was positively correlated with calcium content of the exoskeleton. Thus, the general softening of the population in response to acidification indicated some inhibition of calcium uptake at pH 5.63 or less. This field observation closely matched the laboratory findings of Malley (1980) who demonstrated that Ca^{2+} uptake rates of postmoult *O. virilis* were inhibited by 15–20% at pH 5.75. In their permanently soft state, these crayfish were more vulnerable to damage both from natural causes and from the collection technique. As the pH of L223 declined, the percentage of damaged individuals (i.e. those with broken or missing claws, appendages, or exoskeleton parts) increased (Table 1). No comparable changes in either the percentage of damaged specimens or in carapace rigidity were seen for L240 crayfish.

Although juvenile and adult crayfish showed signs of ionic stress, particularly during the most severe phase of the acidification, growth remained constant throughout the experiment. Three pieces of evidence support this claim. First, the timing and frequency of moulting did not change in response to acidification. Moult periods continued to be marked by the annual appearance of sexually inactive adults early in the summer and by the reappearance of sexually active ones each fall (Table 1). Second, the number of crayfish in the largest size category remained similar from year-to-year until the population became extinct late in 1982, indicating that growth to maximum size had not been affected by pH. Indeed, some of the largest crayfish ever found in L223 were captured in the spring of 1982 when the epilmnion pH was 5.09. Third, apart from a small amount of annual variability, the relationships between carapace length and wet weight (Table 1) remained essentially the same throughout the experiment indicating that the "condition" (Ricker 1975) and growth of *O. virilis* were unaffected by acidification.

France and Graham (1985) have suggested that increased parasitism by the microsporidian *Thelohania contegeani* may have contributed to the demise of crayfish in L223. They reported an average incidence of infected animals in L223 of 1.7% (1979), 6.5% (1980), and 7.7% (1981), but only 0.0–0.4% (1979, 1980) in L240. I found that between 0.1 and 6.4% of the individuals collected from L223 (1980–82) were infected (Table 1) compared with 0.0–10.8% of the crayfish from L240 (1981–85). No data were available to establish *Thelohania* infection rates in L223 before acidification, but values for all years lay within the range observed for the L240 reference population. Naturally high levels of *Thelohania* infection have been reported for other lakes by Sumari and Westman (1969); and Carstairs (1979). In addition, the disease has a long and rather benign incubation period before it kills (Bowler and Brown 1977), suggesting that only a small proportion of total mortality during the final phase of the crayfish population collapse in L223 could have been attributed to this infection.

TABLE 2. Backprojection of the L223 *Orconectes virilis* population age structure during the period of sustained recruitment failure (1979–82) and for 1978, the year immediately preceeding any noticeable acidification effects. Abundance of each cohort was calculated by beginning with the 1982 data and assuming that (1) age dependent mortality rates remained constant and that (2) the differences in total crayfish abundance (diver census estimates) from year-to-year during the collapse were due to the loss of one year class annually, caused by the progression of recruitment failures through the population structure. Egg numbers for 1978 were calculated by estimating the population size of berried females present and their mean egg complement. No estimate of egg numbers was made for 1979–82; other dashes indicate empty year classes.

Year	Spring egg complement	Fall/age-class abundance 0+	1+	2+	3+	Total population size
1982	—	—	—	—	—	0
1981	—	—	—	—	8 000	8 000
1980	—	—	—	24 000[a]	8 000	32 000[b]
1979	—	—	28 300	24 000	8 000	60 300
1978	1 100 000	45 500	28 300	24 000	8 000	105 800

[a]32 000–8 000 = 24 000.
[b]Interpolated value from Fig. 4 (see text).

Lake trout (*Salvelinus namaycush*) predation did not appear to be a significant cause of crayfish mortality either. Although trout in ELA lakes occasionally eat crayfish, they are usually piscivorous or feed on *Mysis relicta* (K. H. Mills, Freshwater Institute, Winnipeg, Man., pers. comm.). *Mysis* disappeared from L223 in 1979 (Nero and Schindler 1983). Thereafter, the trout appeared to feed exclusively on young white sucker (*Catostomus commersoni*) and cyprinids (Mills et al. 1987) which were abundant until 1982.

The persistence of large *O. virilis* in L223 until the final year of the population collapse suggested that juvenile and adult mortality was not greatly affected by acidification. Mortality could not be calculated directly, but could be estimated for a preimpact year (1978) by means of a theoretical reconstruction of population age structure (Table 2; see methods for details). A summary of cohort mortality based on assumed age structure of the L223 crayfish population present in 1978 is given in Table 3.

Results showed that once crayfish were recruited into the population, mortality rates remained low until the animals reached old age (Table 3). The backprojection technique undoubtedly yielded an overestimate of hatchling mortality because many surviving young-of-the-year remained hidden and were not counted in the population totals during the annual SCUBA census. Except for the egg to 0+ age interval, estimates of cohort mortality from backprojection were considerably lower than other values from the literature (Table 3), all of which were derived from length-frequency analysis of age structure.

If the assumption of temporally constant mortality used in the model reconstruction had been false and acidification had decreased the chances of survival in all age classes, the actual population present in 1978 would have contained more old adults and fewer juveniles. Actual mortality rates would have been even lower than those shown in Table 3 and the difference between the model results and conventional calculations of mortality would have been even greater. This evidence supports

TABLE 3. Percentage estimates of annual *Orconectes virilis* mortality. Values from other studies were either reported directly or calculated from data given in each source reference.

Lake (year)	Sex	Percent mortality over the age interval				Reference
		Egg to 0+	0+ to 1+	1+ to 2+	2 to 3+	
223 (1978)	♂ + ♀	95.8	37.8	15.2	66.7	This study
223 (1979)	♂ + ♀	—	62 (1–2)[a]	75 (2–3)[a]	94 (3–4)[a]	France and Graham (1985, table 2)
224 (1979)	♂ + ♀	—	54 (1–2)[a]	64 (2–3)[a]	90 (3–4)[a]	France and Graham (1985, table 2)
239 (1979)	♂ + ♀	—	46 (1–2)[a]	71 (2–3)[a]	87 (3–4)[a]	France and Graham (1985, table 2)
240 (1979)	♂ + ♀	—	52 (1–2)[a]	67 (2–3)[a]	86 (3–4)[a]	France and Graham (1985, table 2)
North Twin (1966–69)	♀	74.6[b]	84.7[b]	62.7[b]	—	Momot and Gowing (1977, table 3)
West Lost (1966–69)	♀	82.5[b]	89.9[b]	31.7[b]	—	Momot and Gowing (1977, table 3)
West Lost (1962–63)	♂	94	50	34	89	Momot (1967, table 4)
West Lost (1962–63)	♀	93	63	69	85	Momot (1967, table 4)
Dock	♂ + ♀	94.6[b]	81.6	44.8	92.7	Momot (1978, table 3)
Shallow	♂ + ♀	89.0[b]	88.5	59.4	91.9	Momot (1978, table 3)

[a]Bracketed values indicate year class interval.
[b]Average of reported values.

the assertion that during acidification it was recruitment failure, not juvenile or adult mortality, that lead to the collapse of the *O. virilis* population in L223. Further, the great disparity between the model results presented here and conventional calculations of mortality, points out the need to validate any technique used to determine population age structure.

Use of *O. virilis* in Acidification Monitoring Programmes

This study has shown that *O. virilis* is susceptible to the early stages of acidification in soft-water lakes. Other species such as *O. rusticus*, *Cambarus robustus*, and *C. bartoni* are comparatively more resistant to acidic conditions (Berrill et al. 1985). In addition to its acid sensitivity, *O. virilis* is easy to identify and is widely distributed in lakes and streams across the northern parts of eastern and central North America, thus making it a good indicator organism for use in acidification monitoring programmes.

Detailed population studies of the type presented here are too labour intensive to permit their general use. However, a progressive softening of the exoskeleton of intermoult animals due to disruption of their calcium metabolism at low pH may provide a reliable basis for documenting early acidification effects on biota that is independent of capture technique. Intermoult crayfish of either sex and any size may be caught in the spring or fall by hand, in traps, or with nets. Exoskeleton rigidity can be measured either by pinching the carapace, or more quantitatively by determining carapace calcium content per unit dry weight or the percentage of its dry weight which is lost on ignition at <500°C.

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A Diver Operated Suction Gun and Collection Bucket for Sampling Crayfish and Other Aquatic Macroinvertebrates

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Davies, I. J. and D. J. Ramsey. 1989. A diver operated suction gun and collection bucket for sampling crayfish and other aquatic macroinvertebrates. Can. J. Fish. Aquat. Sci. 46: 923–927.

A suction gun powered by rubber tubing and a collection bucket with a self-closing lid were developed to assist SCUBA divers in sampling crayfish. Design details of the equipment are reported. Test collections done by hand and with the suction gun each contained a full size range of crayfish and equal proportions of male and female specimens. By comparison, females, young-of-the-year, and juvenile crayfish were poorly represented in catches from baited wire traps. Divers found that using the suction gun was easier, faster, and less damaging to specimens than collecting by hand.

On a mis au point un pistolet à succion relié à un tuyau en caoutchouc et un baquet collecteur muni d'un couvercle à fermeture automatique pour aider les plongeurs autonomes à prélever des échantillons d'écrevisses. On donne des détails sur la conception de l'équipement. Dans les collections faites à titre d'essai à la main et au moyen du pistolet à succion, on retrouvait un éventail complet d'écrevisses de tailles variées et des proportions semblables de spécimens mâles et femelles. Par comparaison, les femelles, les jeunes de l'année et les jeunes écrevisses étaient faiblement représentés dans les prises obtenues au moyen de casiers métalliques appâtés. Les plongeurs ont trouvé que l'utilisation du pistolet à succion était plus facile, plus rapide et causait moins de dommages aux spécimens que la collecte à la main.

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A method for obtaining representative samples of crayfish from a population of *Orconectes virilis* was needed to help evaluate the effects of an experimental lake acidification (Davies 1989). Initially crayfish were sampled from Lake 223 (L223) at the Experimental Lakes Area (ELA), northwestern Ontario by using baited wire minnow traps. The majority of specimens in trap catches were adult males with a carapace length >19.3 mm. By contrast, when crayfish came out of their daytime retreats to forage on the substrate at night, SCUBA divers observed that large numbers of females, juveniles, and young-of-the-year were also present. A hand captured sample of crayfish taken by divers at night contained specimens of all sizes and approximately equal numbers of males and females. This result confirmed the size and sex bias of trapping noted by Capelli (1975) for *O. virilis* in northern Wisconsin lakes. Although collecting by hand was less biased than trapping, it was a slow, uncomfortable job that required that divers work bare-handed for long periods in cold water. Young crayfish were hard to catch because they were small and agile, and larger animals that had recently moulted were soft and easily damaged by hand capture.

As an alternative to sampling crayfish by hand, a simple inexpensive slurp gun powered by rubber tubing was developed to collect specimens by suction. Rather than equipping this gun with an integral sample jar (Smith 1973; Gulliksen and Deras 1975; Tanner et al. 1977), a separate holding container with a self-closing lid was designed and built so that divers could collect large numbers of animals and keep them safe from damage, without having to constantly return to shore.

Design details for both the gun and collecting bucket are given below, along with notes on their use and a comparative evaluation of their performance.

Slurp Gun

The gun (Fig. 1A–E) consists of three subassemblies: barrel, piston, and headpiece.

The barrel is a Plexiglas (clear acrylic plastic) tube 70 mm outside diameter × 6 mm wall × 610 mm long. At one end of the barrel is a flap valve (Fig. 1C) made from a circular piece of sheet rubber (tire inner tube), cut to form four pie-shaped segments that remain joined around their circumference. A flat ring of brass or Lexan (polycarbonate) plastic, fixed to the end of the barrel by four countersunk machine screws, holds the flap valve in place and affords it some protection from abrasion by rocks. A narrow ring of acrylic plastic cemented to the outside of the barrel (with Dichloromethane) approximately one-third of the way up from the valve forms a convenient hand grip to prevent slippage when cocking or emptying the gun.

Aluminum rod (12.7 mm) diameter × 685 mm long), threaded for 100 mm on one end and 150 mm on the other, supports the piston and handle assembly (Fig. 1A). Two rubber stoppers (No. 11), bored to fit over this rod and spaced 50 mm apart with their tapered ends facing, form the piston. Steel washers and machine nuts on either side of the stoppers hold them in place on the 100 mm-long threaded segment of the rod. In this configuration the diameters of the front and rear sections of the piston can be independently adjusted (by tightening or

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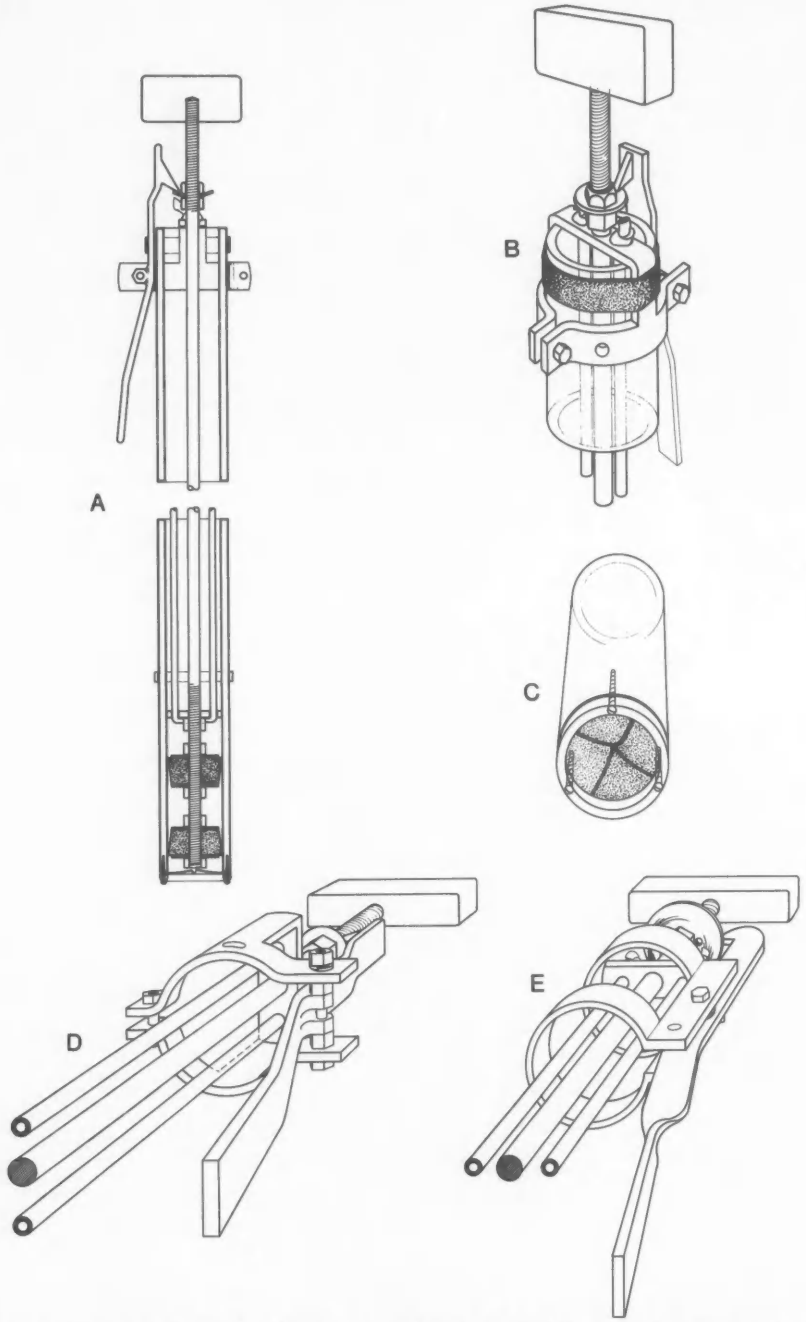

FIG. 1. (A) Longitudinal section view of the gun. Note that the headpiece assembly has been rotated 90 degrees for the purpose of illustration. (B) Standard headpiece, showing top detail. (C) Barrel end and flap valve detail. (D) Standard headpiece, showing trigger detail. (E) Stainless steel headpiece. In all drawings latex tubing is not shaded; stippled areas are rubber.

loosening the machine nuts) to make the stoppers fit snugly in the barrel. At the other end of the rod, a drilled and tapped rectangle of acrylic plastic (100 mm × 60 mm × 25 mm thick) serves as a handle to allow the operator to cock the gun and expel the contents of the barrel. The gun is cocked by depressing the piston until the trigger engages its catch (a cupped

washer, fixed in position on the rod by a pair of machine nuts).

The headpiece (Fig. 1B) supports the trigger assembly, guides and retains the piston, and provides attachment points for the ends of a loop of latex rubber tubing (11 mm outside diameter × 3 mm wall × 500–550 mm long) that powers the piston. Two designs are illustrated. The first design (Fig. 1B, 1D) can be easily made, with aid of a welding torch, from 25 mm × 6 mm steel stock. Two pieces of steel, bent to conform to the curve of the barrel, are joined at either end by bolts to form a clamp. The piston rod passes through a hole drilled in the middle of a rectangular "U" shaped bracket (Fig. 1B) that is welded to each half of the clamp. This bracket holds the piston squarely inside the barrel and acts as a backstop to retain the piston after the gun is triggered. Holes in this bracket provide attachment points for the latex tubing. Because this rear bracket bears against the long axis of the barrel when the latex tubing is under tension, the clamp portion of the headpiece need only fit snugly around the barrel, thus preventing the plastic barrel from becoming deformed or cracked by excess clamp pressure. A small piece of steel, in the shape of an obtuse triangle, welded to one end of a length of 25 mm × 6 mm stock, forms the trigger sere. A sleeve bushing (Fig. 1D) welded to the midpoint of this stock permits attachment of the trigger to one of the headpiece clamp bolts. Below the bushing, the handle portion of the trigger is bent outward in a slight "S" shape to keep it parallel to the barrel, but allow sufficient movement for the sere to clear its engagement and release the piston rod when the trigger handle is depressed. A heavy band of rubber (tire inner tube) around the outside of the headpiece (Fig. 1B) acts as a trigger return spring.

A modified headpiece made from stainless steel is shown in Fig. 1E. Although this headpiece is more costly and more difficult to construct than the basic model, it is corrosion proof. The barrel clamp consists of two bands of steel welded to vertical support pieces of rectangular stock. A single bolt and wing nut compresses the bands around the barrel and provides a pivot for the trigger which can be cut and bent, as shown, from a single piece of heavy sheet steel. This style of trigger also may be used with the previously described headpiece. A piston guide/backstop is welded across the top band of the barrel clamp. Holes drilled in the backstop, on either side of the piston guide, serve as attachment points for the latex tubing. As with the previous design, a heavy band of rubber around the headpiece acts as a trigger spring.

Collection Bucket

The collection bucket, shown in Fig. 2A–C, may be used in conjunction with the slurp gun or by itself, as a self-closing,

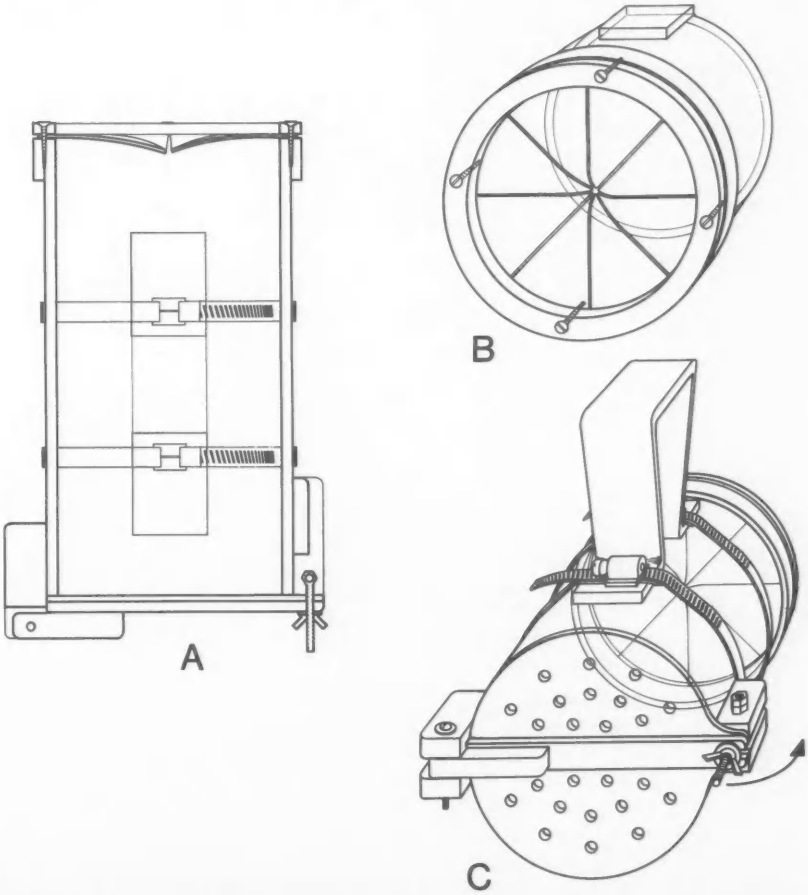

FIG. 2. (A) Top view of the collection bucket. (B) Front view, showing entrance cover detail. (C) Rear view, showing end plate, hinge, catch, and handle detail.

protective, sample container. Because it is made almost entirely from clear plastic, divers can easily see the number of organisms they have sampled and their condition.

The body of the collection bucket is made from a piece of 151 mm outside diameter × 6 mm wall acrylic plastic tube ≃280 mm long. A disc of 0.75 mm thick cellulose acetate butyrate (or any other plastic that is stiff but not rigid) is cut across several diameters to within 10 mm of its edge to create a number of pie-shaped wedges that form a self-closing entrance for the bucket (Fig. 2B). The disc is held securely against one end of the container body by an acrylic support ring. Four machine screws, spaced at 90 degree intervals and countersunk into this ring, thread into holes which have been drilled and tapped into one end of the tube. The bottom of the bucket (Fig. 2C) is hinged on one side and held closed by a bolt and wing-nut catch on the other side so that it can easily be opened or closed by divers wearing wetsuit gloves. Holes drilled in the acrylic plastic bottom plate are small enough to retain the sample organisms but large enough to allow sand, fine sediment, or water to drain from the bucket. The hinge support is made from three rectangles of 11-mm thick acrylic plastic cemented (with Dichloromethane) to the outside of the bucket. The two outer parts of this support extend beyond the edge of the bucket to accomodate the movable portion of the hinge which is a longer bar of acrylic plastic, glued along most of its length to the back of the bottom plate. A bolt, passing through holes drilled in this bar and the supports on either side, acts as the pivot for the hinge. On the opposite side of the container two additional rectangles of 11-mm thick acrylic, spaced 6 mm apart by a shorter third piece, are glued to the outside surface of the tube. An eye bolt, positioned in the space between these plastic supports and held in place by a machine bolt, pivots to one side away from a notch in the bottom plate, as indicated by the arrow (Fig. 2C), to release the bottom and open the container. In the closed position the bottom is fastened shut by tightening the wing-nut and washer on the eye bolt against the bottom plate. The bucket handle is fashioned from a 50-mm wide × 6-mm thick strip of acrylic plastic that has been heated with a propane torch or heat gun and bent to the desired shape. The ends of the handle are fastened to the body of the bucket by large diameter gear type hose clamps made of stainless steel.

Method of Use

The gun is cocked by holding the barrel at arm's length in one hand and pushing against the handle with the other hand to force the piston forward in the barrel, until the trigger engages its catch. The end of the gun barrel can then be moved to within a few centimetres of the target organism and the piston released by squeezing the trigger handle. Recoil of the piston causes the gun to jump forward, while inrushing water opens the flap valve and sucks up the target specimen. Once the piston reaches the top of its travel, the flow of water stops and the flap valve at the end of the barrel closes, thus retaining the sample. To transfer captured organisms to the collection bucket, the barrel end is pressed lightly against the acetate wedges on the bucket top to force them slightly open, then the gun is recocked. Water expelled from the barrel pushes the flap valves open on both the gun and bucket and transfers the gun contents to the container. Excess water entering the bucket escapes through the holes in the bottom and from between the entrance wedges, but samples are retained. Because water flow does most of the work, damage to the specimen is minimal.

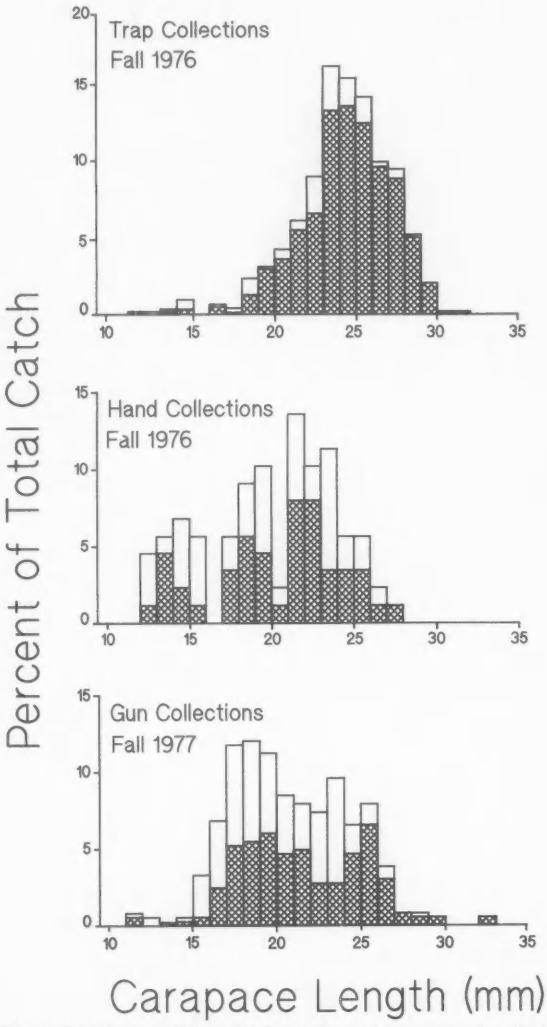

FIG. 3. Distribution of *O. virilis* size (measured as carapace length) in samples obtained by three capture techniques in L223. The shaded portion of each stacked bar represents the abundance of male crayfish in a length class, expressed as a percentage of the total catch for that collecting method. Unshaded portions of the bars represent female crayfish abundance in the same way.

Crayfish can be collected most easily at night by a team of two divers. One diver uses the gun while the other, holding an underwater light, acts as a spotter and carries the collection bucket. Few organisms react to the light as long as the divers remain behind its beam. The collecting operation requires strict organization and a short training period to ensure safety and success. A major point of safety in using the gun is that both the operator and the helper should stay clear of the piston handle when the gun is triggered. This danger can be minimized if the divers maintain constant relative position.

The degree of suction generated by the gun may be regulated by adjusting the tension of the latex tubing. The gun functions most efficiently when the tubing is adjusted to provide just enough suction to capture the target organism, but minimize the quantity of unwanted sand, gravel, and debris which is also

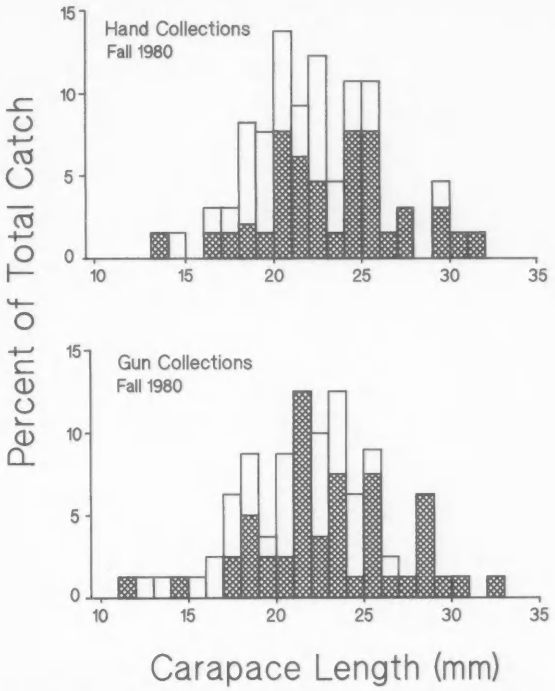

FIG. 4. Distribution of *O. virilis* size (measured as carapace length) in a paired test of diver-taken hand collections and slurp gun collections in L240. The shaded portion of each stacked bar represents the abundance of male crayfish in a length class, expressed as a percentage of the total catch for that collecting method. Unshaded portions of the bars represent female crayfish abundance in the same way.

collected. A gun adjusted for maximum tension is tiring to use and the extra effort required to cock it may induce tendonitis in the operator's elbow.

Evaluation of Performance

To determine the efficiency of the slurp gun, samples of crayfish from L223 captured by baited wire minnow traps, hand collections, and gun collections during a period of apparent population stability were compared. In the fall of 1976, 85.9% (±3.5%, 95% confidence limits) of the crayfish caught in traps (N = 638) were male (Fig. 3). The majority of these males were adults. Hand collections of crayfish (N = 88), taken that same fall (Fig. 3), contained males and females in approximately equal numbers (52.3% male ± 14.0%). Juveniles (15.0–19.3 mm carapace length) and young-of-the-year (<15.0 mm carapace length) were well represented in the hand collections, but comparatively rare in the trap sample. The percentage of male crayfish (51.6% ± 7.0%) and the relative abundance of juveniles in fall 1977 slurp gun collections (N = 372) compared favourably with values observed for the hand collections of the previous year (Fig. 3). Young-of-the-year were poorly represented in the gun catch because sampling was done a month earlier in the season, at a time when young crayfish tended to remain hidden in the gravel and rocks of the lake bottom during the early stages of their lives. Thus, fewer of the young were seen by the divers.

Crayfish with broken carapaces and damaged or missing chela were occasionally found in all samples. The natural abundance of these damaged crayfish in the population was estimated to be 3.1% from the trap samples. By comparison, 9.1% of individuals in the hand-collected sample and 6.4% of crayfish in the gun collection were damaged. These results indicated that while some specimen damage can be expected to occur when animals are collected with a slurp gun, fewer animals are injured by this technique than by hand collecting.

A more rigorous comparison of the hand and slurp gun collecting methods was done in L240 at ELA in the fall of 1980, using divers skilled in both techniques. Total sampling time for each trial was noted. Figure 4 shows that both hand and gun collections yielded approximately the same picture of *O. virilis* population structure. The hand collection (N = 65) contained 55.4% ± 17.2% male specimens, compared to 60.0% ± 12.5% males in the gun collections (N = 80). These estimates were not significantly different ($p<0.05$). Young-of-the-year crayfish appeared to have been undersampled by both techniques because they tended to remain hidden and were therefore less vulnerable to capture.

Although sample sizes were similar, the rates of capture differed considerably for the two collecting methods. Hand capture yielded an average of 1.7 specimens per minute, compared to a rate of 3.1 crayfish per minute for the slurp gun. Many specimens were able to elude hand capture, but more than 90% of all capture attempts with the slurp gun were successful. Thus, in addition to being more convenient and less damaging to specimens than hand collecting, use of the slurp gun also doubled the diver's collecting efficiency.

The gun and collection bucket described above have been used at ELA to sample crayfish, dragonfly nymphs (*Aeshna* sp.), green frog tadpoles (*Rana clamitans melanota*) and, with limited success, slimy sculpins (*Cottus cognatus*). During the 8 yr that this equipment has been in use, each piece has required only minor repairs. Guns usually need new latex tubing and a piston adjustment annually, along with an occasional replacement of the rubber flap valve and trigger band. The acetate top of the collection bucket tends to break after several hours of use, but new tops are inexpensive, easy to make and can be quickly changed in the field.

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Significance of Mature Male Parr in a Small Population of Atlantic Salmon (*Salmo salar*)

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The spawning population of Atlantic salmon, *Salmo salar*, (mature male parr and adults (anadromous salmon)) were assessed in the River Bævra, central Norway, when the river was treated with rotenone in November 1986. The spawning population of adults consisted of 15 males and 19 females. The spawning population of males consisted of 167 mature male parr per adult male. The effective population size of adults was small; $N_a = 33.5$ individuals. The presence of mature male parr theoretically increased the effective population size to $N_a = 71.7$ individuals. This increase indicated that mature male parr brought the effective population size above a recommended minimum ($N_a = 50$) to ensure long term viability.

La population de géniteurs de saumon de l'Atlantique (*Salmo salar*) (tacons mâles matures et adultes (saumon anadrome)) a été évaluée dans la rivière Baevra dans le centre de la Norvège lorsque la rivière a été traitée au rotenone en novembre 1986. La population de géniteurs adultes était composée de 15 mâles et de 19 femelles. La population de géniteurs mâles étaient composée de 167 tacons mâles matures par mâle adulte. L'effectif réel d'adultes était faible : $N_a = 33,5$ individus. La présence de tacons mâles matures a porté, en théorie, l'effectif réel à $N_a = 71,7$ individus. Cette augmentation a montré que des tacons mâles matures portaient l'effectif réel au-delà d'un minimum recommandé ($N_a = 50$) afin d'assurer une viabilité à long terme.

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Atlantic salmon, *Salmo salar*, display great variability in age at maturation both within and among populations. As many as 80% of the male parr may become mature (Myers 1984), while adults (anadromous Atlantic salmon) may mature after 1–4 yr at sea (Jones 1959). The coexistence of alternative maturation phenotypes within populations, indicates that maturation of male parr is not a single frequency-independent optimum (Gross 1984; Myers 1984). Myers (1986) demonstrated by using game theory (Maynard Smith 1982) that multiple evolutionary stable equilibria may exist between the proportion of mature male parr and the proportion of adult males.

In a recent study Saunders and Schom (1985) suggested that... "the great variability in age and life stage of spawners, including the presence of sexually mature male parr, allows Atlantic salmon to persist as small populations in which effective population size is increased by this variability." However, they were not able to quantify the significance of the mature male parr in the effective size of the spawning population. From a genetics point of view, Allendorf and Ryman (1987) suggested that at least 25 females and 25 males (effective population size; $N_a = 50$) was necessary to ensure long term viability.

To my knowledge no data is available concerning the total number of mature individuals in a spawning population of Atlantic salmon. In the present study I was able to check the entire number of spawners in a small population of Atlantic salmon. Thereby I could test the hypothesis that mature male parr contribute genetically bringing the reproductively active population above the minimum for continued existence.

Materials and Methods

The River Bævra, central Norway (63°01′N, 8°35′E), was treated with rotenone in November 1986. At this time the water temperature was approximately 2°C. The plan was to kill all salmon in the river and thereby eliminate the monogenean parasite *Gyrodactylus salaris*. This parasite was recorded for the first time in the river in August 1986. Atlantic salmon were spawning as the rotenone treatment was carried out. Nets were set across the river at four sites to collect drifting dead adult (anadromous) salmon. In addition the entire river was checked for dead adults, and a random sample of dead parr ($n = 334$) was collected. The entire spawning run of adults (15 males and 19 females) in 1986 was collected. The river morphology made it possible to sample dead fish almost everywhere in the river. Sampling of parr was carried out in all habitats to obtain an estimate of mature males for the entire population. The sample of parr was estimated visually to constitute roughly 5% of parr ≥ 1 yr in the river, giving an estimated total number of parr of 6680.

Total length (0.1 cm), sex, and degree of sexual maturity of all collected fish were recorded. Parr were aged by using otoliths and scales. There was no discrepancy between these two ageing techniques. Freshwater age and sea age of 26 adult

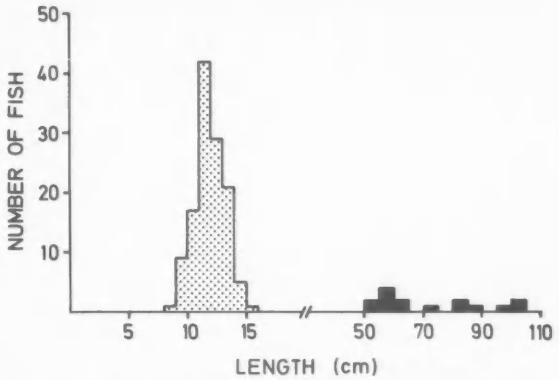

FIG. 1. Length distribution of sampled mature parr ($n = 125$; stippled bars) and mature adult males ($n = 15$; solid bars) in the River Bævra November 1986. Note the break in the length scale.

salmon were determined from scales, the remaining eight adults could not be read.

The numbers of adults and mature male parr were used to calculate generation length, effective population size, and rate of inbreeding (Hedrick 1983). In estimating the generation length I used length specific fecundity of Atlantic salmon from the literature (Pope et al. 1961; Baum and Meister 1971; Thorpe et al. 1984). The generation length (T) was calculated as:

$$(1)\quad T = \frac{\Sigma\, x\, l_x f_x}{\Sigma\, l_x f_x},$$

where l_x is the probability of surviving from birth to a particular age class (x), and f_x is the average number of female offspring produced by females of this age class. The effective population size in one spawning season (N_a) was calculated as:

$$(2)\quad N_a = \frac{4\, N_m\, N_f}{N_m + N_f},$$

where N_m is the number of breeding males, and N_f is the number of breeding females. With overlapping generations, effective population size (N_e) can be estimated by

$$(3)\quad N_e = T\, N_a$$

assuming a constant number of spawners, where T is generation length and N_a is the number of individuals born per year which survive to reproductive age. Rate of inbreeding in one generation was calculated as:

$$(4)\quad \Delta F = \frac{1}{2\, N_e}$$

Results

The total count of adult males and females in 1986 (15 and 19 individuals, respectively), revealed an effective population size of adults in one spawning season to be $N_a = 33.5$ individuals (Equation (2)). This estimated effective population size of adults is below that recommended by Allendorf and Ryman (1987). The generation length of females was estimated to be $T = 4.4$ yr (Equation (1)). With overlapping generations, the effective population size of adults was estimated to be $N_e = 147$ individuals (Equation (3)). These figures give a rate of inbreeding of $\Delta F = 0.015$ in one spawning season and, assuming a constant population size, $\Delta F = 0.0034$ per generation in the whole population (Equation (4)).

Mature male parr predominated among the total of mature males in the River Bævra (Fig. 1). The proportion of mature male parr increased significantly ($X^2 = 37.58$, 2 *df*, $P < 0.001$) from 31% in age group 1 to 100% in age group 3 (Table 1). In total, 75.8% of male parr $\geq 1+$ were sexually mature. The number of parr was reduced by approximately 90% from age group 2 to age group 3. Simultaneously the sex ratio increased significantly from approximately 1.0 to 5.5 in favour of males ($G_H = 15.75$, 2 *df*, $P < 0.001$).

From the estimated total number of parr in the River Bævra (6680 individuals), and taking into account the observed age distribution and male:female ratio within each age class (Table 1), the total number of male parr was estimated to be 3340 individuals. According to the observed maturation of males within each age class, the total number of sexually mature male parr in the entire population was estimated to be 2500 individuals. This meant there were approximately 167 mature male parr per adult male in the potential spawning population of males in the River Bævra.

If mature male parr were incorporated into Equation (2) without taking into consideration that they may be less successful spawners, the effective population size increased from $N_a = 33.5$ for adults to 75.4 individuals. This revealed that N_a became larger than the value recommended by Allendorf and Ryman (1987). With overlapping generations, effective population size also increased, and was estimated to be $N_e = 332$ (Equation (3)). This figure is theoretically the highest effective population size for the population of Atlantic salmon in the River Bævra. These figures give a rate of inbreeding (Equation (4)) of $\Delta F = 0.0066$ in one spawning season and, assuming a constant population size $\Delta F = 0.0015$ per generation in the whole population.

TABLE 1. Number, length (millimetres) and sex ratio of immature and mature Atlantic salmon parr, in the River Bævra, November 1986. ns = $P > 0.05$ that sex ratio different from 1.0, * = $P < 0.001$.

	1+		2+		3+	
Group	Males	Females	Males	Females	Males	Females
Number immature	18	25	22	140	0	4
Mean length (SD)	87.5(8.2)	88.3(6.4)	116.7(8.5)	123.8(8.5)	—	137.3(9.1)
Number mature	8	0	95	0	22	0
Mean length (SD)	93.3(3.5)	—	117.9(9.6)	—	134.3(9.9)	—
Percent mature	30.8	0	81.2	0	100.0	0
Male:female-ratio	1.04^{ns}		0.84^{ns}		5.50^{*}	

TABLE 2. Number of adult Atlantic salmon with smolt ages 3 or 4 yr in the River Bævra 1986.

	Smolt age			
Sex	3	4	Unreadable	Mean
Males	10	2	3	3.2
Females	14	0	5	3.0

Mean smolt age of adult males was higher than that of females (Table 2). The difference was, however, not significant ($P>0.05$). The sex ratio in adults was not significantly different ($P>0.05$) from 1:1 (male:female = 15:19 = 0.79).

Discussion

This is the first study of a river where it has been possible to count the total number of adult spawners and estimate the proportion of mature male parr in a wild population of Atlantic salmon. The results show that the spawning population in the River Bævra was estimated to consist of 167 mature male parr per adult mature male. The presence of the monogenean parasite *Gyrodactylus salaris* may have affected this figure. Johnsen and Jensen (1986) examined Norwegian rivers in several years for occurrence of *G. salaris* and found that the density of juvenile Atlantic salmon was reduced during the second year after infestation. However, as the interval between the first observation of *G. salaris* and rotenone treatment of the River Bævra was only 3 mo, the infestation by *G. salaris* probably had little effect on the results. The result may also be biased by erroneous estimate of the number of parr sampled. An autumnal change in behavior and distribution has been demonstrated in juvenile Atlantic salmon (Rimmer et al. 1983): as the water temperature falls below 10°C the juveniles are found mostly in sheltered stations within the streambed. In the River Bævra dead juveniles mostly accumulated in pools, although they were also found in other habitats (runs and riffles) throughout the river bed. The behavior of the juveniles at low water temperatures may, however, have lead to an underestimation of the total number of parr.

The effective population size (N_e) of Atlantic salmon in the River Bævra was between 147 individuals (without mature male parr) and 332 individuals (with mature male parr) which theoretically were the lowest and highest effective population sizes, respectively. A more exact determination of the effective population size within this range depends on several factors: (1) the ability of mature male parr to stimulate adult females to spawn, (2) the ability of sperm of male parr to fertilize eggs and produce viable offspring, (3) the ability of mature male parr to fertilize eggs in competition with an adult male, and finally (4) the number of male parr contributing to fertilization of the eggs. It is known that mature male parr under simulated natural conditions may successfully mate with adult females in the absence of adult males (Myers and Hutchings 1987), and that eggs fertilized by mature male parr can produce viable offspring (Jones and King 1950; Thorpe and Morgan 1980; Hutchings and Myers 1985). In a study of spawning activity of Atlantic salmon, Hutchings and Myers (1988) demonstrated that mature male parr successfully fertilized eggs of an adult female in competition with adult males, and that a single male parr fertilized on average 5% of the eggs in a redd. In total, male parr fertilized approximately 23% of the eggs in a redd when the ratio of male parr:adult male reached 20:1. Above this ratio, Hutchings and Myers (1988) experimentally demonstrated that the proportion of eggs fertilized by parr stabilized. Assuming this result is relevant under natural conditions, the effective population size in the River Bævra in 1986 ($N_m = 315$, $N_f = 19$) was estimated to be $N_a = 71.7$ individuals (Equation (2)), and $N_e = 315$ individuals (Equation (3)). This N_a value is within the range of effective population size recommended for population maintenance in hatcheries (Allendorf and Ryman 1987). Furthermore, the N_e value is in accordance with the population size of sockeye salmon ($N_e \approx 200$) from Lake Azabachye, Kamchatka (Altukhov 1982, and references therein). Gall (1987) stated that if the rate of immigration is much larger than $1/4N_e$, it will override the effect of genetic drift in small populations. When using 0.03 as the straying rate in Atlantic salmon (Stabell 1984) this is much greater than the observed $1/4N_e$ ($=0.00026$) in River Bævra. This indicates that immigration (strays) theoretically may effect the genetic structure of the Atlantic salmon in the River Bævra.

In the River Bævra the majority (>75%) of male parr older than 1+ become sexually mature. This result lies within the range of variation in populations of Atlantic salmon from North America (Dalley et al. 1983; Myers et al. 1986) and Sweden (Eriksson et al. 1979; Lundqvist et al. 1986). The considerable reduction in number of parr from age group 2+ to 3+ indicates that 3 yr is the most common smolt age of Atlantic salmon in the River Bævra. Calculation of smolt age from adult salmon supports this conclusion. As more than 80% of male presmolts ≥2+ are sexually mature, this indicates that most of the male adult salmon in the River Bævra matured previously as parr. This conclusion is supported by the following facts: (1) no mature male parr residing in freshwater are older than the age of smoltification, and (2) 4-yr old smolts were recorded among adult males, while no 3+ immature male parr were captured in 1986. Lundqvist et al. (1988) demonstrated that for Baltic salmon the survival to adulthood from smolts of mature male parr was about 2%. If this survival rate of mature male parr was true in the River Bævra, then females should have vastly outnumbered adult males as more than 80% of potential male smolts were mature. However, in the River Bævra the sex ratio within parr and adults was approximately 1:1. This indicated that the survival of mature male parr to adulthood in this river was considerably higher than reported by Lundqvist et al. (1988). Thus, mature male parr may potentially contribute to the genetic make-up of the population twice, once as parr and once (or more, if they succeed in being repeat adult spawners) as adults. This fact will also increase the effective size of the population (Saunders and Schom 1985).

To conclude, the proportion of mature male parr in the small population of Atlantic salmon in the River Bævra increased the effective population size above the minimum for continued existence, and helped ensure successful reproduction and continuation of the population.

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Biennial Reproductive Cycle of Blue King Crab, *Paralithodes platypus*, at the Pribilof Islands, Alaska and Comparison to a Congener, *P. camtschatica*

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Pribilof Island blue king crab (BKC; *Paralithodes platypus*) were sampled by beam trawl in May and August of 1983 and April 1984 to determine timing of reproductive events. Biennial reproduction was found to be the result of slow ovarian growth in large, multiparous females, while smaller primiparous females are often able to spawn in two consecutive years. Mating and egg extrusion occur in late March to early May and eggs hatch in mid-April of the following year, consequently, the embryonic period and rate of development is approximately 12 mo, similar to that of its congener the red king crab (RKC; *P. camtschatica*). Comparison of the reproductive output of the two species revealed that despite the 2 yr ovarian cycle, BKC only produce 20–30% more dry egg mass at any carapace length than do RKC, a substantially smaller difference than previously calculated. One year after molt, females of both species are not significantly different in dry body weight over a size range of 100–140 mm carapace length, but RKC have produced about three times more dry ovarian weight than BKC of comparable size, suggesting that biennial reproduction in BKC may be the result of energetic limitations.

Des spécimens du crabe de l'île Probilof (*Paralithodes platypus*) ont été capturés au chalut à perche en mai et en août 1983, ainsi qu'en avril 1984, afin de déterminer l'époque du déclenchement de la reproduction. On a constaté que la reproduction bisannuelle était le résultat d'une croissance ovarienne lente chez les grosses femelles multipares, et que les femmes primipares plus petites sont souvent aptes à frayer au cours de deux années consécutives. L'accouplement et la ponte ont lieu de la fin de mars au début de mai et les oeufs éclosent à la mi-avril de l'année suivante, ce qui suppose un développement embryonnaire d'une durée d'environ 12 mo, que l'on observe aussi chez un congénère de l'espèce, le crabe royal (*P. camtschatica*). Une comparaison de la reproduction des deux espèces a révélé qu'en dépit d'un cycle ovarien de deux ans, le crabe de l'île Pribilof ne produit que de 20 à 30 % plus d'oeufs, en poids sec, pour toutes les longueurs de carapace, que le crabe royal, ce qui représente une différence très inférieure aux résultats antérieurs. Bien qu'une année après la mue, le poids corporel sec des femelles des deux espèces ne diffère pas sensiblement pour des longueurs de carapace variant entre 100 et 140 mm, on a cependant prélevé chez le crabe royal une masse ovarienne dont le poids sec était trois fois supérieur à celui relevé chez un crabe de l'île Probilof de taille comparable, ce qui indique que la reproduction bisannuelle chez cette dernière espèce pourrait être le résultat de limitations énergétiques.

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For several decades, large lithodid crabs of the genus *Paralithodes* have formed the basis of an important fishery in the North Pacific and Bering Sea (Otto 1981, 1985). Since 1980 there has been a dramatic decline in populations of the red king crab (RKC; *P. camtschatica*), traditionally the primary component of the king crab harvest. As a result, a greater proportion of the catch now consists of a lesser-known relative, the blue king crab (BKC; *P. platypus*, (Otto 1986). At the same time, plans by the Minerals Management Service (U.S. Dept. of Interior) to lease tracts of the southeastern Bering Sea for oil and gas development highlighted the need for biological data on species like *P. platypus* in order to evaluate potential impacts to crab resources and the fisheries.

Previous studies of the reproductive cycle in *P. platypus* have concluded that it differs from that of its congener (Sasakawa 1973, 1975a; Otto et al. 1980; Jensen et al. 1985; Somerton and MacIntosh 1985), yet differ in their interpretation of the cycle and the timing of reproductive events. Female *P. camtschatica* reproduce annually; females molt, mate and extrude a new clutch of eggs in the spring shortly after eggs from the previous year hatch (Marukawa 1933; Wallace et al. 1949). However, substantial interannual variation in the percentage of ovigerous female *P. platypus* within the mature population has been reported (Otto et al. 1980) suggesting a two year reproductive cycle for this species. Sasakawa (1975a) inferred from tagging experiments in the western Bering Sea that the cycle consists of a 19-mo period of embryonic development (ovigerous condition) followed by a 5-mo period between the hatch of old eggs and extrusion of new ones. Somerton and MacIntosh (1985), in studies of BKC at the Pribilof Islands, concluded that females were ovigerous for 14–15 mo, and that biennial reproduction was due to a 2-yr ovarian cycle. They proposed that this may be an adaptive strategy enabling BKC to expend more energy per brood and also reduce the risks associated with an

annual molt, and speculated that the species has a longer reproductive life to help offset less frequent reproduction.

In the current study, the reproductive biology of female blue king crab from the Pribilof Islands was investigated through histological examination of ovaries, examination of eggs and shell condition, gonosomatic indices, and larval stage-frequency data. The fine spatial scale of sampling around the Pribilof Islands (over 400 stations) was intended to possibly show onshore-offshore movement of adult crab around the islands during the reproductive season, and to study larval distribution and benthic juvenile habitat as part of a study of the species' island ecology (Armstrong et al. 1985).

Materials and Methods

Extensive sampling of blue king crab was conducted in May and August of 1983 and April of 1984 near the Pribilof Islands (57°00′N, 170°00′W), using a 3-m plumb staff beam trawl (described in Armstrong et al. 1985 and modified from Gunderson and Ellis 1986). All processing of crab body dimensions, dissections of ovaries, and fixation and drying of egg and ovarian samples was done aboard ship. Carapace length (CL) and weight of all specimens were recorded as well as shell condition (SC) in accord with standard National Marine Fisheries Service (NMFS) categories as follows: SC1, soft shell (just molted); SC2, new shell (shell clean, spines sharp; molted within the past several months); SC3, old shell (molted previous year); SC4, very old shell (greater than 1 yr since last molt). To determine molt condition in specimens not sacrificed for analysis of ovaries, the dactyl of a walking leg was broken and examined for evidence of an underlying new shell. This was done to learn if females rated as SC 3 or 4 were near molt and therefore likely to extrude eggs that spring. Egg condition (color; eyed/uneyed) and an estimate of clutch size were noted for ovigerous specimens, and a small portion of eggs (<0.5% of total clutch) was fixed in Bouin's solution and later transferred to 70% ethanol. Several females from each shell and egg condition category were dissected and a small piece of ovary (<0.5% of total ovary) was also fixed in Bouin's solution, transferred to 70% ethanol and later embedded in paraffin, sectioned at 8 μm, and stained with Weigert's hematoxylin and eosin *Y*. The remaining eggs were carefully stripped from the pleopods with forceps, and the eggs, ovary, and body were dried separately at 50°C to constant weight in shallow, perforated aluminum pans.

Embryonic stage and rate of development were determined from preserved egg samples examined under a dissecting scope and compared with developmental stages illustrated for *P. camtschatica* in Marukawa (1933). Ova diameters were measured using an ocular micrometer on a compound microscope at 100× magnification; 5–10 of the largest and roundest ova were measured and the average diameter calculated. A gonosomatic index (GSI) was calculated by dividing the dry ovary weight by the total dry body weight (less eggs) and multiplying by 100 (dry body weight was found to correspond much better to carapace length than ash-free weight). Similarly, an egg index (EI) was calculated by dividing the dry weight of egg clutches by the dry weight of the remaining body including ovary and multiplying by 100.

In order to determine the timing of egg hatch, plankton samples were collected with twin 60-cm diameter bongo nets with 505-μm mesh, fished by oblique tows to a depth of 80 m or to 5 m above bottom, whichever was less (Armstrong et al. 1985). Larval abundance was calculated by area (No. per 100 m^2) to compensate for variable depths of tows. Samples were fixed in 5% formalin and zoeae staged according to Hoffman (1968).

RKC collected during the three cruises to the Pribilof Islands were similarly processed aboard ship. Additional specimens were collected in June and August 1982, and February, April, and June 1983 along the North Aleutian Shelf on ships of opportunity and by NMFS personnel on annual groundfish surveys. These specimens were frozen whole and transported to Seattle, Washington where they were dissected and dried as described above.

Results and Discussion

This study of reproductive biology of BKC provides new information on oogenesis, embryonic development and duration, and direct comparisons to a congener, RKC. Another study of female BKC at the Pribilof Islands by Somerton and MacIntosh (1985) provided information that led them to modify Sasakawa's (1973, 1975a) proposed ovarian cycle, and to suggest hypotheses to account for biennial reproduction as a strategy different from that of RKC.

Mature female BKC caught in spring of 1983 and 1984 were located primarily east of St. Paul Island (the northernmost island in the Pribilof group), at depths of 40–70 m on a mixed mud–sand substrate (Armstrong et al. 1985). In August 1983, female king crab were more widely distributed between St. Paul and St. George Islands but were still very close to the Pribilof group relative to the total extent of shelf area in the southeastern Bering Sea.

Ovarian Cycle

Primiparous Females, Annual Spawning

The size of female BKC at 50% maturity was estimated by Somerton and MacIntosh (1983) to be 96 mm CL at the Pribilof Islands, and by Otto et al. (1980) to be between 101–105 mm CL. Some of the female crab larger than 95 mm CL caught during our surveys had not yet spawned (no external eggs or empty egg cases on the pleopods), but were probably approaching their primiparous molt. These animals comprised 33% of the females between 95 and 105 mm CL caught in May 1983 and April 1984; all specimens larger than 104 mm CL showed evidence of prior spawning. Within this same size interval of 95–105 mm (n = 24), 50% of the females carrying eyed eggs or empty egg cases (n = 8) also had fully developed ovaries (GSI $\bar{x}$ = 15.3%; ova diameter $\bar{x}$ = 766 μm) and were in premolt condition, indicating that they were ready to spawn for a second consecutive year. The proportion of these annual spawners dropped to 7% of those in the range 105–120 mm CL, and only 1.6% at sizes greater than 120 mm.

This conclusion that a large proportion of primiparous females can spawn in two consecutive years is consistent with the findings of Otto et al. (1980), who found in four consecutive years that most females between 101–110 mm were ovigerous while among those greater than 111 mm a high percentage of egg-bearing females occurred only every other year, in a pattern consistent with a biennial cycle. The annually-spawning females in our samples averaged 112 mm CL and, based on very limited molt increment data of Sasakawa (1975a), would be about 118 mm CL following the next molt, a size where biennial spawning is the norm. Egg extrusion in two consecutive years is likely a feature of small body size which enables females to grow suf-

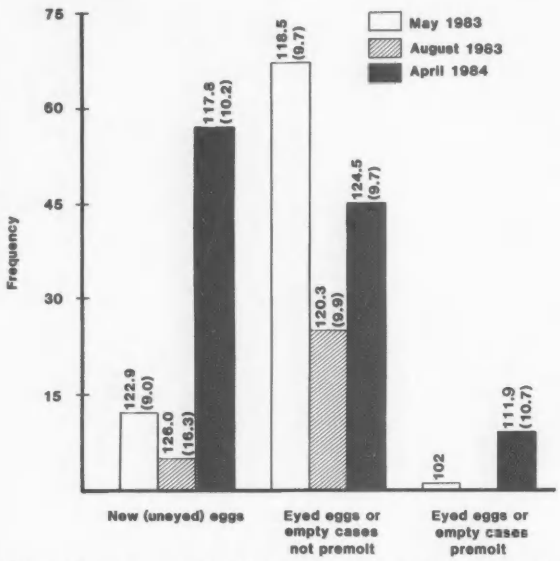

FIG. 1. Frequency, egg condition, and mean carapace length in millimetres (SD) for female blue king crab caught at the Pribilof Islands.

ficient ovarian and somatic tissue to molt annually. Annual spawners with large ovaries carrying eyed eggs in April 1984 at a mean size of 111.9 mm CL were significantly smaller than those also with eyed eggs but small ovaries ($\bar{x}$ = 124.5 mm CL; *t*-test, $p<0.001$; GSI $\bar{x}$ = 5.7%; Fig. 1).

Multiparous Females, Biennial Spawning

Over 90% of the females carrying eyed eggs or empty egg cases in May 1983 and April 1984 showed no sign of impending molt and had small ovaries (GSI $\bar{x}$ = 5.3%; Fig. 3), indicating that they had extruded eggs the previous spring but were not ready to molt and spawn again. These animals in the middle of the biennial cycle averaged 118.5 and 124.5 mm CL in May 1983 and April 1984, respectively (Fig. 1).

Calculation of GSIs revealed at least two temporally distinct stages of reproductive growth for each sampling period; this is to be expected in an annually reproducing population composed of individuals which spawn biennially because not all individuals are breeding in the same year. While calculation of the GSI might appear to allow a reliable assessment of an individual's reproductive condition, this must be used in conjunction with shell condition (SC), egg development, and direct examination of the ovary to accurately determine where an animal is in the reproductive cycle. A simplistic example would be an individual with an extremely small ovary and GSI. Depending on shell condition, size, and the presence or absence of eggs, it could fall into one of several categories: an immature specimen, one that has just extruded eggs, or possibly a senescent individual. Our sample of 239 female crabs spanning two consecutive spawning and hatching seasons allowed these factors to be correlated with plankton data to provide the following scenario for BKC biennial reproduction, typical of most of the female population.

Female BKC molt, mate, and extrude a clutch of eggs in late March through mid-April (46% of 124 female BKC sampled in mid-April 1984 were SC2 with new eggs, Fig. 1). Following extrusion, the spent ovary consists primarily of connective tissue, accessory cells, immature ova and degenerating ova (Fig. 2b), and comprises only 1.4% (GSI) of the dry body weight (Fig. 3). Immature ova appear to remain intact and probably develop in the subsequent year, while those that underwent vitellogenesis but did not attain full size appear to degenerate and be reabsorbed.

By late summer (August; month 4 since extrusion) the GSI has reached 3.4% (Fig. 3), the ovaries are brown or pink in color, and the largest ova contain some yolk and are about 500 μm in diameter (Fig. 2c and 3). Females are SC2 and carry eggs with well-developed embryos that possess eyestalks and a telson (Fig. 2h,i).

By April of the following year (month 12 of cycle) eggs are eyed and hatching and the mean GSI is 5.3%; individual ova are approximately 500 μm in diameter, not having increased in size over winter (Fig. 3). These animals have now reached the same stage in the reproductive cycle as those with eyed eggs or empty cases caught the previous spring. Following through again to August (month 16 of cycle), females now have old shells (SC3), empty egg cases, and large, purple ovaries. Ova have developed quickly since April, are full of yolk and average 700 μm in diameter; the GSI is about 9% but oogenesis is still not complete (Fig. 2e and 3). Finally, females caught in the following spring (month 24 of cycle) in premolt condition with large ovaries round out the cycle. The GSI averages over 15% and ova are nearly 800 μm in diameter (Fig. 2a and 3). Although still less than the 1000 μm crossectional width reported for newly extruded eggs (Sasakawa 1975b; Somerton and MacIntosh 1985), these ova were clearly ready to be extruded and the smaller size was probably due to shrinkage during dehydration for embedding and sectioning.

Duration of Embryogenesis

Our data indicate that the 19-mo embryonic period proposed by Sasakawa (1973, 1975a) is not accurate for Pribilof Island BKC, as noted by Somerton and MacIntosh (1985). If a 19-mo cycle was true, then in order for eggs to hatch in April as observed, they must be extruded in November, 1.5 yr earlier. At the Pribilof Islands, all ovigerous females caught in the spring of 1983 and 1984 had new, clean shells (SC1 or 2) and carried newly extruded eggs, or had old shells (SC3) and empty egg cases or eyed eggs in the process of hatching. According to Saskawa's (1975a) hypothesis, eggs extruded in November would presumably contain embryos that are at least moderately differentiated 6 mo later in April; yet no evidence whatever was found for a "midpoint" spring embryo in our samples, and thus 19 mo for embryogenesis can be discounted.

Nor is there evidence within our study to support the conclusion of Somerton and MacIntosh (1985) that BKC at the Pribilof Islands have a 14–15 mo embryonic period in which eggs extruded the previous February-April hatch the following May and June. In both 1983 and 1984 eggs were extruded primarily in April based on shell condition (SC1, 2; often soft, always thin, clean, and spines very sharp), and very little differentiation of embryos (a few cellular divisions, no gastrula). Some portion of the larval year class also hatched in April of both years (Fig. 2j) as evidenced by occurrence in zooplankton samples and presence of SC3 females with empty egg cases. In 1984 between April 12 to 30, larval BKC were measured at densities of 2000 to 4000 per 100 m^2 of sea surface, and all were S1 zoeae found south of the 0°C surface isotherm midway between St. George and St. Paul Islands. In early May 1983, most larvae (4000 per 100 m^2, with peak values of 13 000–

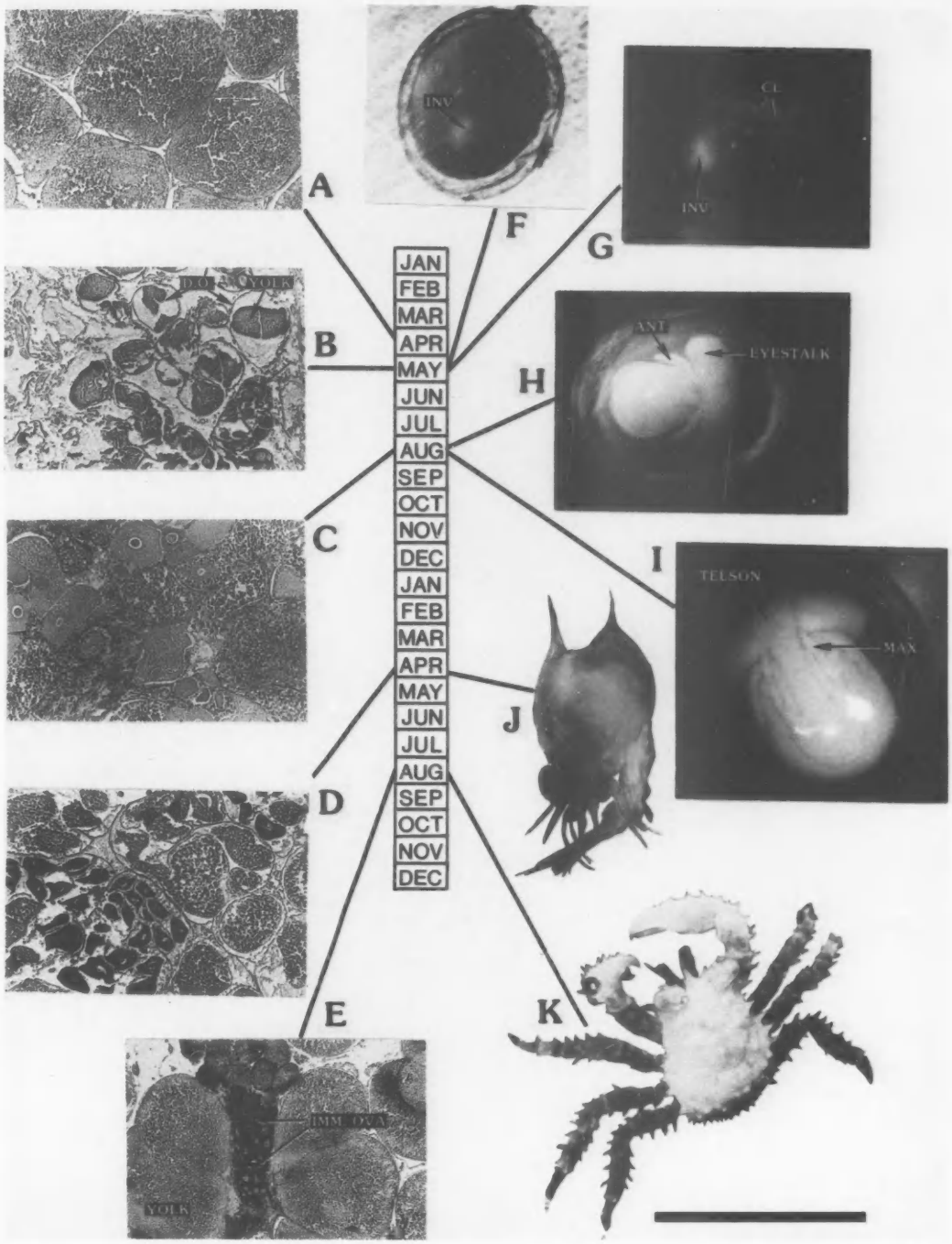

FIG. 2. Ovarian growth and egg development of blue king crab: (a) section of well-developed ovary, scale bar = 1 mm; (b) section of ovary from a female carrying newly extruded eggs; only immature or degenerating (D.O.) ova and connective tissue remain, scale bar = 1 mm; (c) ovary of female carrying eggs in August; some ova are vitellogenic, scale bar = 1 mm; (d) ovary from a female carrying eyed eggs, scale bar = 1 mm; (e) large ovary from August female carrying empty egg cases, showing immature (IMM) ova and large, yolk-filled ova, scale bar = 1.5 mm; (f) recently extruded egg showing initial invagination (INV), scale bar = 1.25 mm; (g) recently extruded egg with invagination (INV) and cephalic lobes (CL) beginning to show, scale bar = 1.25 mm; (h) egg from ovigerous specimen caught in August showing embryo with prominent eyestalks and antennae (ANT), scale bar = 1.12 mm; (i) large embryo with a well-developed telson from August 1983; maxilliped (MAX), scale bar = 0.9 mm; (j) first stage blue king crab zoea caught in early May, 1983, scale bar = 2.4 mm; (k) first instar of blue king crab, scale bar = 5 mm.

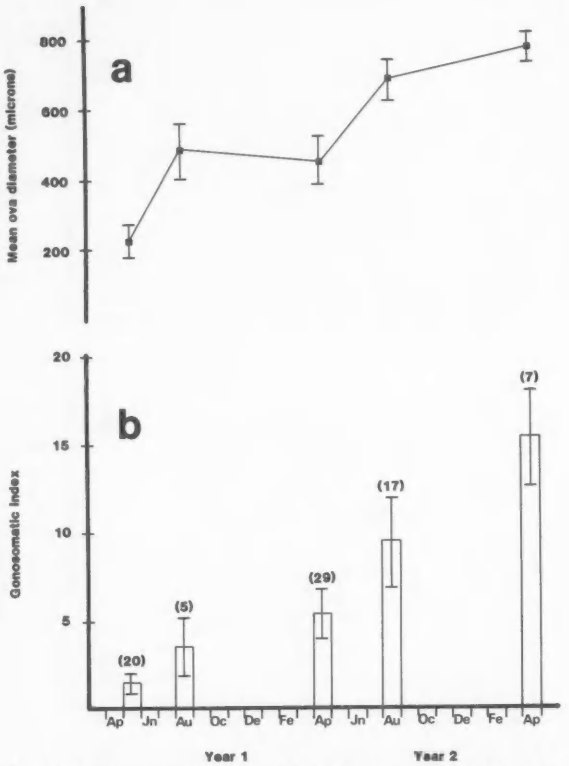

FIG. 3. Ovarian growth of a hypothetical cohort of female blue king crab over a 2-yr period following egg extrusion: (a) mean ova diameters ± 1 SD; (b) mean gonosomatic indices and SD; number of females in parentheses. Data are those actually collected during this study on two reproductively distinct cohorts of the female population (essentially those with and without eggs at any point in time), and arrayed on a time line to portray development of ovaries during a biennial reproductive cycle.

18 000 per 100 m^2; Armstrong et al. 1985) were S1 but by the middle of the month 36% of the population had molted to S2 and by the third week of May almost 70% were S2 (Fig. 4). Armstrong et al. (1985) estimated that the duration of zoeal stages for *P. platypus* is 2.5–3 wk, therefore the population found molting to S2 was probably hatched in mid-April of 1983.

Further evidence that BKC larvae hatch around the Pribilof Islands in April (rather than May and June) is provided by Armstrong et al. (1983) who found a mixture of S1 and S2 zoeae in May 1976 zooplankton samples, S4 zoeae in June 1978, and only megalopae at high densities in July 1982. In August 1983, no zoeae or megalopae were taken in over 50 plankton tows but large numbers of first and second instars (Fig. 2k) were caught on the benthos in areas of heavy bivalve shell deposition near the islands (Armstrong et al. 1985), indicating larval development was completed prior to mid-August. Thus, we interpret these data to indicate that embryonic development for BKC (egg extrusion to hatch) is approximately 12 mo, in accord with embryonic development of RKC (Marakawa 1933; Wallace et al. 1949).

The rate of embryo development from May to August 1983 corresponds to that described by Marukawa (1933) for RKC and this, coupled with larval data, also indicates that the embryonic period for the two species is similar. The eggs extruded by biennial spawners from late March to early May (most by mid-April) by August already have well-developed eyestalks, antennae, and telson (Fig. 2h,i), and hatch the following spring in April.

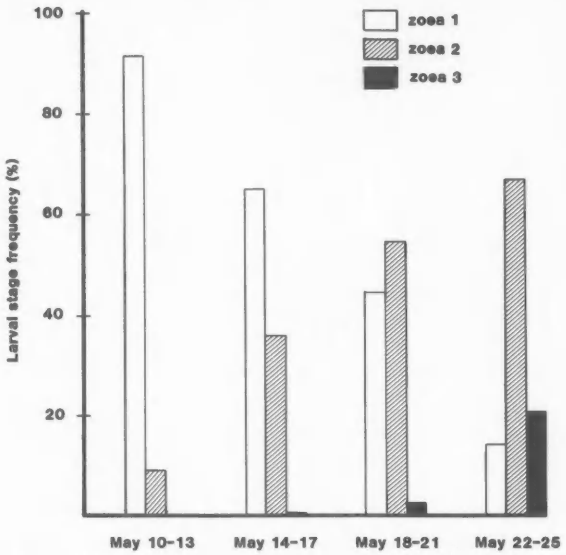

FIG. 4. Blue king crab larval stage frequency for May 1983.

Embryogenesis that only requires 12 mo dispells a problem noted by Somerton and MacIntosh (1985) who concluded the species has a 14 to 15-mo embryonic period yet noted that some females manage to spawn in two consecutive years. They could only suggest that embryos of some females are able to complete development within 12 mo; in our view this is always the case. Part of the dilemma faced by Somerton and MacIntosh (as they noted) was the need to construct a calendar year chronology of reproductive events from data collected over 5 yr and arrayed in 4 mo (April, July, October, and February). When no females with empty egg cases were found in April samples and none with eyed eggs were found in July, they chose the time of hatch as the midpoint between these 2 mo, and concluded that embryogenesis requires 14–15 mo. Similarly, few females with uneyed eggs in February (most carried eyed eggs) and the lack of females with empty egg cases (females yet to molt and extrude eggs) in April was taken as evidence that egg extrusion was complete by that time. A potential problem in interpreting the chronology of extrusion and maturation of embryos could result from using only crab pots to collect females in April 1979. Crabs nearing molt and postmolt crab do not feed (Warner 1977) and are unlikely to respond to baited traps, so data from pots are probably biased against certain reproductive stages (e.g. females about to molt and extrude eggs and probably those who extruded within a week or less) which are critical to setting time boundaries for egg extrusion and hatch.

Biennial Reproduction: Adaptation or Limitation?

BKC and RKC share similar reproductive features in several respects (e.g. seasons of molt and mating, duration of embryonic development) but differ in one important feature: the latter spawns annually while the former usually spawns biennially.

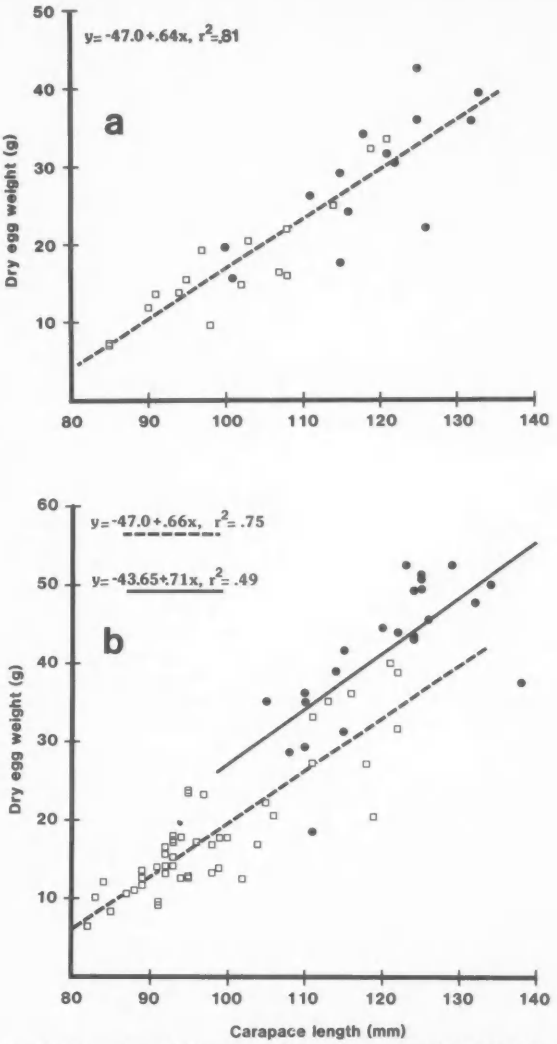

FIG. 5. Regressions of dry egg weight on carapace length for blue king crab (solid circles) and red king crab (open squares). (a) Eyed eggs, no difference between species found so common regression line shown; (b) recently extruded egg clutches; solid line, blue king crab, broken line, red king crab.

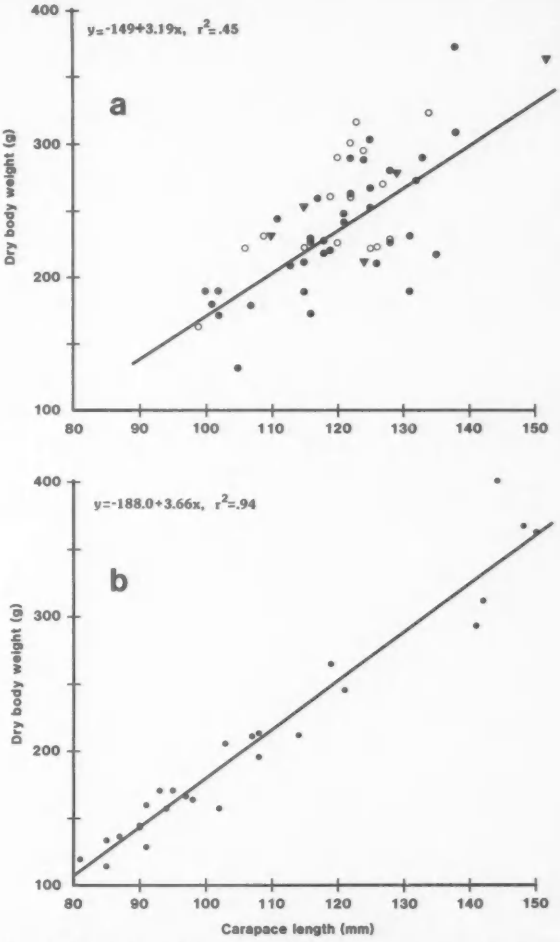

FIG. 6. Regressions of dry body weights (less eggs or ovary) on carapace length for female king crab. (a) Blue king crab. Triangles, approximately 4 mo after molting; black circles, 12 mo; open circles, 16 mo. Regression line fitted to 12-mo data points. (b) Red king crab, approximately 12 mo after molting.

This 1 or 2-yr cycle seems an intrinsic feature and difference between the two that could be viewed as an adaptive feature of the reproductive strategy or a limitation caused by physiological constraints.

If the duration of embryonic development was either 19 mo (Sasakawa 1975) or 14 to 15 mo (Somerton and MacIntosh (1985) (i.e. greater than a year) then a biennial cycle would be a consequence of the limitation imposed by the presence of external eggs and the need to delay molt until larvae hatch. If eggs requiring a development time substantially greater than 12 mo are extruded as soon as the previous ones hatched, then reproduction, including molting and breeding, would quickly become asynchronous with the seasons and deleterious in terms of larval survival and growth (assumably best in spring and summer in terms of food supplies and higher water temperatures). Biennial reproduction would serve as a means to recalibrate reproductive events to the spring as an adaptation to embryogenesis that exceeds a year, but we have shown that the embryonic period is 12 mo for BKC and therefore not responsible for the biennial cycle.

The perspective that biennial reproduction by BKC is an adaptive strategy was generally taken by Somerton and MacIntosh (1985) in an interesting comparison of the two species. They reasoned that BKC is as reproductively fit as RKC despite a 2-yr spawning cycle because the former: (1) produces a much greater volume of eggs and thus expends more energy per spawning; (2) produces larger larvae that may have a survival advantage over RKC and; (3) lives longer. It seems reasonable that a larger larva might have a survival advantage; however, longer reproductive life and a higher energy expenditure per spawning for BKC is speculative based on existing data.

Somerton and MacIntosh (1985) used egg volumes and curvilinear size–fecundity relationships (revised from Haynes 1968) for RKC to compare egg clutch volumes of the two spe-

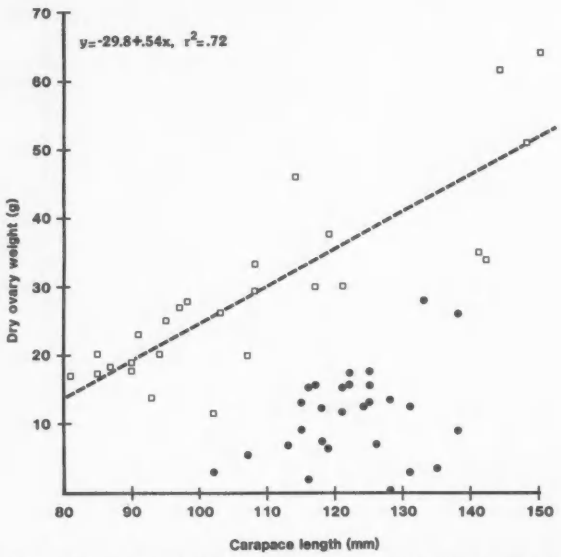

FIG. 7. Dry ovary weights of red king crab and biennially-spawning blue king crab carrying either eyed eggs or empty egg cases. For both species approximately 12 mo have elapsed since their last molt and egg extrusion. Open squares and fitted broken lines, red king crab; black circles, blue king crab. Because of the weak correlation (r^2 = 0.11) the fitted line for blue king crab has not been included.

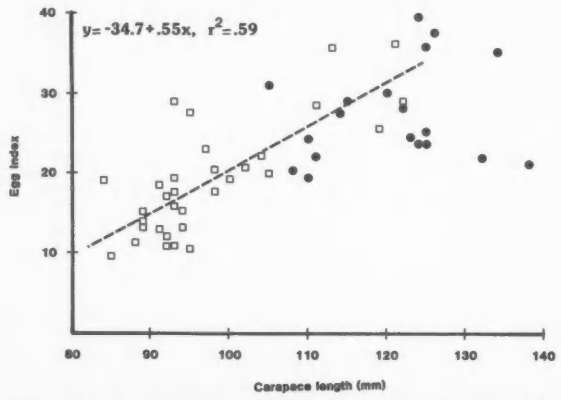

FIG. 8. Egg indices (dry egg weight divided by total dry body weight, including ovary, × 100) of red and blue king crab with recently extruded egg clutches (SC1 or 2; little differentiation of embryos). Open squares, red king crab; black circles, blue king crab. Regression line from red king data only.

cies, and calculated nearly a three-fold greater volume for smaller (100 mm CL) female BKC than RKC; a ratio that decreased to 1.4:1 by 120 mm CL. In addition to the probable multiplicative errors inherent in calculating a clutch volume from an individual egg volume, another tenuous part of the calculation was the prediction that fecundity of small RKC is about 50% less than BKC at 100 mm CL when virtually none of Haynes' (1968) data are for females that small. They suggested that this substantially greater energy output helps offset the 2-yr spawning cycle as compared with annual spawning of RKC.

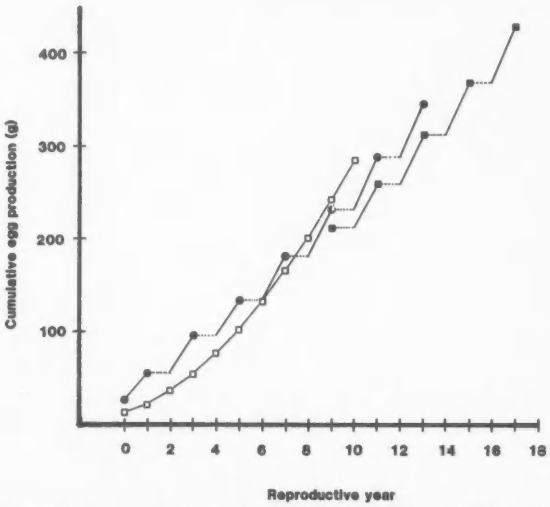

FIG. 9. Predicted cumulative lifetime dry egg weight production for red and blue king crab, using fitted regression lines from Fig. 5b and molt increments of 5.1 mm for red king crab (open squares) over 10 yr, and 5.2 mm (black squares) and 6.8 mm (black circles) for blue king crab over 17 and 13 yr, respectively. Adult size range 99–144 mm for blue king crab and 84–133 mm for red king crab; red king crab reproducing annually and blue king crab first spawning in two consecutive years and subsequently reproducing biennially. Since the estimated production of BKC at 5.2 and 6.8 mm molt increments is very similar up to year 8, only a portion of the former is graphed.

A primary consideration in brood size in brachyuran crabs is the limited volume available inside the exoskeleton for the developing ovary (Hines 1982); anomurans would presumably be subject to similar allometric constraints. Since adult BKC and RKC are very similar morphologically (Somerton 1985), a three-fold difference in clutch volume seems unlikely unless small RKC carry partial clutches. Regressions of the dry egg weight of eyed eggs on CL showed no difference between the two species (Fig. 5a). However, regressions of dry egg weight of newly extruded egg masses on carapace length (Fig. 5b) suggest that BKC indeed produce a greater amount of egg (initially at extrusion) at all sizes than RKC, but at 100 mm CL we predict the ratio of BKC:RKC is only 1.4:1, rather than 2.9:1 as estimated by Somerton and MacIntosh (1985). A comparison of the maximum GSIs of premolt specimens reveals virtually the same ratio of BKC to RKC, with BKC averaging 15.3% (Fig. 3) and RKC 12.1% (SD = 0.02; n = 26); however these premolt BKC values must be used with caution as they are from annual, not bienniel, spawners and it is not known whether maximum GSIs differ between these two reproductive groups. It seems likely that BKC at least partly make up for less frequent spawning (relative to RKC) by producing larger clutches at each molt, but not of the magnitude calculated by Somerton and MacIntosh (1985).

We do not believe that biennial reproduction of BKC is an adaptive strategy but rather a consequence of an energetic limitation wherein larger, multiparous females are generally unable to produce both somatic and ovarian tissue adequate for molting and spawning within a 12-mo period. If we compare the regressions of dry body weight on CL of BKC and RKC carrying eyed eggs or empty cases from recently-hatched eggs in the spring (Fig. 6a,b) there is no significant difference between

species (t-test, $p>0.05$); in both cases 1 yr has elapsed since their last molt and weight gain in somatic tissue is the same. Yet in that same period RKC over a wide size range have produced three times more dry weight of ovarian tissue than BKC, and are ready to spawn for a second consecutive year (Fig. 7). Thus, the total energy gain over a 1-yr period is substantially less for BKC, suggesting some sort of physiological or energetic limitation rather than a strategy of accumulating twice as much energy as proposed by Somerton and MacIntosh (1985).

Although August data for female BKC with new eggs (about 4 mo since extrusion) is rather sparse, it is interesting to compare the dry body weights of BKC 4, 12, and 16 mo after spawning (Fig. 6a). It appears that the first summer following egg extrusion is devoted almost entirely to somatic growth, and the body weight remains unchanged for the next 12 mo. The greatest increase in ovarian weight occurs primarily in the second year of the cycle when the GSI goes from about 5.3 to 15% (Fig. 3). This is taken as evidence that BKC have slower ovarian growth than RKC and are generally unable to complete both full ovarian growth and somatic growth within a single year. We see the ability of small, primiparous BKC to often spawn in two consecutive years as additional, albeit circumstantial, evidence that the biennial cycle is due to energetic constraints. If an adaptive advantage to biennial spawning exists it seems unlikely that small individuals would opt to spawn annually. In addition, plots of egg indices (EI; egg to body weight) versus CL show that egg production per unit body length increases with larger size for RKC and less so for BKC (Fig. 8). If BKC live in areas with less or poorer quality food resources, or if feeding activity is reduced by colder water temperatures or a shorter growing season, it may not be energetically feasible for large females to complete both ovarian and somatic growth sufficient to molt and extrude eggs annually. Bull and Shine (1979) noted that low frequency reproduction can be characteristic of poorer quality habitat or shorter growing season; in general BKC are found in colder waters than RKC (Slizkin 1971) and in April 1984 bottom water temperatures around St. Paul Island were $-0.5°$ to $-1.0°C$, much colder than usually encountered by RKC (Fukahara 1985).

Another means by which BKC could make up for infrequent spawning is through a longer reproductive life span. Somerton and MacIntosh (1985) calculated that the reproductive life of RKC is about 10 yr, and for BKC could be either 13 or 17 yr based on two versions of very limited data from Sasakawa (1975a; molt data $n = 5$). Using our regressions of new-egg dry weights on CL for BKC and RKC (Fig. 5b), we calculated a hypothetical cumulative lifetime egg production for BKC and RKC. Adult size ranges were taken from Somerton and MacIntosh (1985) with BKC between 99–144 mm CL and RKC 84–133 mm CL; BKC were presumed to have spawned in the first two consecutive years of reproductive life. Based on molt increments of 5.1 and 6.8 mm CL for RKC and BKC, respectively, the former would produce a cumulative individual total of 282 g dry eggs in 10 yr of sexual maturity whereas a BKC would produce 346 g eggs over a 13-yr reproductive life (Fig. 9). At a molt increment of 5.2 mm, BKC would have an estimated reproductive life of 17 yr and would produce 429 g. These values may be somewhat overestimated by extending a linear regression to the largest size range in the population (>130 mm CL) for which we have little data. Sasakawa (1975b) and Somerton and MacIntosh (1985) suggest an asymptotic relationship between CL and fecundity, and our own data (Fig. 7 and 8) shows increasing variability and suggests that ovary and egg production decline at larger sizes.

Somerton and MacIntosh (1985) are likely correct that longer reproductive life helps to compensate for biennial reproduction based on our calculations of cumulative egg production. Clearly though, more molt increment data are needed for BKC to determine both reproductive life span and output. If, for instance, BKC have substantially greater molt increments than RKC then their life span calculated from the size frequency plots shown by Somerton and MacIntosh (1985) would be shorter and their cumulative egg output less than our estimate. A larger average molt increment than RKC would also necessitate greater somatic growth in a proportionally larger volume making annual reproduction all the more difficult.

Many biennially reproducing species have additional energy expenditures such as breeding migrations or egg brooding which may make low frequency reproduction advantageous (Bull and Shine 1979). Somerton and MacIntosh (1985) saw biennial reproduction of BKC as consistent with such a strategy in which energy normally put into an annual molt is shunted instead to greater ovarian production; by accumulating energy for twice as long as an annual spawner they would be able to produce twice as large an egg clutch. We believe both notions are incorrect, and that allometric constraints dictate that a comparable internal body volume is available for ovaries of each species no matter how long it takes to fill. Although BKC spawn more egg weight per unit size than do RKC (Fig. 5b), it takes them twice as long to produce only 20–30% more.

We believe that biennial reproduction of BKC is a consequence of physiological and energetic constraints incurred by the species in a harsh environment, but do not known whether it is intrinsic to the species even if more favorable conditions (e.g. of food and temperature) are encountered elsewhere throughout its range. The observation that small females can reproduce in two consecutive years is consistent with a hypothesis of energetic impairment of reproduction that comes with larger size and the need for proportionately greater somatic growth. For whatever reasons of size-dependent metabolism and feeding rate, food supply, temperature, etc., large *P. platypus* are not able to produce a mature ovary annually and this fact strikes us as more a disadvantage than an adaptation comparable with yearly reproduction.

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Variability, Tuning, and Simulation for the Doubleday–Deriso Catch-at-Age Model

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This paper presents a method for estimating the variances of biomass estimates made using the nonlinear least squares catch-at-age model. The estimates begin with the standard covariance matrix of parameters estimated using nonlinear least squares and is therefore an extension of usual methods. In this paper the catch-at-age model is tuned to independent survey estimates of biomass. If the variances of these survey estimates are known, it is possible to estimate an optimal value for the weighting variable λ in the nonlinear least squares. The methods are applied to the walleye pollock (*Theragra chalcogramma*) fishery in the Eastern Bering Sea. Results from this study generally support the theoretical interpretation of λ as a ratio of variances. When the model is constrained to recent survey biomass estimates, estimates of the coefficient of variation of biomasses in earlier years are large. Also, the results largely depend on what constraints on selectivities are assumed. A simulation was performed assuming catches-at-age are distributed as lognormal random variables and that selectivities are all estimated. Results from the simulation indicate that modelled biomass estimates for early years are questionable, and probably seriously biased. However, the simulation generally validated the analytic estimates of the variance of modelled biomass estimates.

L'auteur du présent document présente une méthode d'évaluation des variances des estimations de la biomasse effectuées au moyen d'un modèle non linéaire des moindres carrés des prises en fonction de l'âge. Les estimations débutent avec la matrice standard des covariances des paramètres évalués au moyen de la méthode non linéaire des moindres carrés et constitue donc une extension des méthodes courantes. Dans le présent document, le modèle des prises en fonction de l'âge est réglé sur des évaluations d'enquête indépendante de la biomasse. Si les variances de ces évaluations d'enquête sont connues, il est possible d'évaluer une valeur optimale pour la variable (λ) de pondération du modèle non linéaire des moindres carrés. Les méthodes s'appliquent à la pêcherie de la goberge de l'Alaska (*Theragra chalcogramma*) dans l'est de la mer de Béring. En général, les résultats de cette étude soutiennent l'interprétation de (λ) comme un rapport de variances. Lorsque le modèle est limité aux estimations de la biomasse effectuées dans le cadre d'une étude récente, les estimations du coefficient de variation de la biomasse au cours des premières années sont importantes. De plus, les résultats dépendent en grande partie des contraintes sur la sélectivité qui sont supposées. Une simulation a été effectuée en supposant que les prises en fonction de l'âge sont réparties comme des variables aléatoires log-normales et que les sélectivités sont bien estimées. Les résultats de la simulation montrent que les estimations de la biomasse modélisées pour les premières années sont douteuses, et qu'elles sont énormément biaisées. Toutefois, la simulation a validé en général les estimations analytiques de la variance des estimations modélisées de la biomasse.

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There has been a recent explosion in the number of models available to perform sequential population analysis on catch-at-age data. This explosion appears to have begun with the least squares analysis proposed by Doubleday (1976), who was apparently attempting to fit the "separable" model proposed earlier by J. G. Pope (unpubl. data). This was followed by Paloheimo (1980); Pope and Shepherd (1982); Fournier and Archibald (1982); Dupont (1983); Deriso et al. (1985); Gudmundsson (1986); Methot (1986); and Deriso et al. (1989). Collie and Sissenwine (1983) propose a catch-at-age model for survey indices.

From the model fitting point of view these models fall roughly into two classes: least squares, and maximum likelihood estimation based on multinomial probabilities. The methods of Doubleday (1976); Paloheimo (1980); Pope and Shepherd (1982); Deriso et al. (1985); Gudmundsson (1986); and Collie and Sissenwine (1983) all use least squares, and the methods Fournier and Archibald (1982); Dupont (1983); and Methot (1986) all use maximum likelihood. Of course, least squares solutions are also maximum likelihood under the normal errors assumption.

This paper is a contribution to the theory of separable, nonlinear least squares catch-at-age models as developed by Doubleday (1976); Deriso et al. (1985); and Deriso et al. (1989). The principal advantage of the Doubleday–Deriso model is that it is standard nonlinear least squares, pure and simple. Therefore it can be fitted using commercially available software packages, and the average assessment scientist will have considerable intuition concerning the model fitting process, and how anomalies in the data might affect modelling results.

This paper extends the variance estimates of parameter estimates available from the nonlinear least squares to provide "analytic" formulas for estimating the variance of modelled total and fishable biomass. Deriso et al. (1985) used bootstrap-

ping to provide variance estimates of modelled biomass. Although the bootstrapping method should be robust, it is also time consuming compared with direct calculations. Also, directly calculated variance estimates are more convenient for, and conceptually related to, the process of model tuning.

In this paper the Doubleday–Deriso model is tuned to independent estimates of fishable biomass. For this method of tuning I show how optimal estimates of the weighting variable λ can be arrived at. This method of tuning appears to be consistent with the analytic estimates of the variance of fishable biomass. A method is also described for the Monte Carlo simulation of the model. Finally, I apply the analysis to the walleye pollock (*Theragra chalcogramma*) fishery in the Eastern Bering Sea.

Least Squares Catch-at-Age Model

Let $i=1,\ldots,y$ be the year index, and $j=1,\ldots,a$ be the age index for some species which has a nonzero ages of catch. Let

c_{ij} = the observed catch in numbers at age,

F_i = the instantaneous fishing mortality rate for fully available ages (i.e. ages for which $s_j = 1$),

s_j = the selectivity for age j fish such that the assumption of "separability" holds, i.e.,

$F_{ij} = F_i s_j$ = the instantaneous fishing mortality rate on age j fish during year i,

N_{ij} = the total population numbers at age, and

$U_{ij} = F_{ij}(1-\exp(-M-F_{ij}))/(M+F_{ij})$ = the exploitation rate on age j fish in year i, assuming an instantaneous natural mortality rate of M.

It follows that

$$N_{i+1,\,j+1} = N_{ij}\exp(-M-F_{ij}),$$

and predicted catch would be

$$\hat{c}_{ij} = U_{ij}N_{ij}.$$

This model contains $p = 2y+2a-1$ parameters:

$$b = \{F_1,\ldots,F_y,s_1,\ldots,s_a,N_{11},\ldots,N_{1a},N_{21},\ldots,N_{y1}\}$$

with $m = ya$ observations. Parameters can be estimated by minimizing the residual sum of squares:

$$SSC = \Sigma_{ij}(log(\hat{c}_{ij}) - \log(c_{ij}))^2.$$

This model was described rather completely by Doubleday (1976), but at that time did not receive the full attention it deserved.

Deriso et al. (1985), in a definitive paper, described several ways of performing least squares analysis on catch-at-age data. As the title of their paper implies, their emphasis was on constraining solutions using auxiliary information in addition to the catch-at-age data. Deriso et al. (1985) define auxiliary information as either additional data (e.g. survey estimates, effort data) or additional model structure (e.g. a stock–recruitment relationship). The focus of their paper was important because Doubleday (1976) and others had shown that catch-at-age data alone was insufficient to estimate absolute abundance.

Because fishery stock assessments tend to focus on total and fishable biomass estimates, and because in my corner of the world auxiliary information often comes in this form, I prefer tuning the Doubleday–Deriso model using independent survey estimates of fishable biomass $\{S_i^f\}$. In the model, total and fishable biomass are estimated by $\hat{B}_i = \Sigma_j N_{ij}w_j$ and $\hat{B}_i^f = \Sigma_j N_{ij}s_j w_j$, respectively where w_j is the average weight at age j. Note that the series $\{S_i^f\}$ will typically be far less complete than the catch data series $\{c_{ij}\}$.

Following Deriso et al. (1985) the augmented sum of squares to be minimized is:

$$SST = SSC + SSB$$
$$= \Sigma_{ij}(log(\hat{c}_{ij}) - \log(c_{ij}))^2 + \lambda\,\Sigma_i(\log(\hat{B}_i^f) - \log(S_i^f))^2.$$

Here λ is an unknown constant that, assuming independent normally distributed errors, should theoretically be

$$\lambda = \text{var}[\log(c_{ij})]/\text{var}[\log(S_i^f)],$$

for minimum variance parameter estimates. For simplicity var$[\log(S_i^f)]$ is assumed to be the same for all of the surveys.

There are, of course, many different ways that the model might be constrained. For example, the surveys might be measures of total biomass, B_i, rather than fishable biomass. Or the survey estimates (S_i^f) may be relative indices proportional to fishable biomass, in which case *SSB* would become

$$SSB = \lambda\,\Sigma_i(\log(q\hat{B}_i^f) - \log(S_i^f))^2,$$

where q is a parameter of proportionality. As far as I can see, only minor changes in the calculations would be required to accommodate such modifications. For example, if q is estimated it must be included in the calculations that lead to the covariance matrix of parameter estimates. When using a model that estimates q, it should be noted that q may be greater or less than 1.0.

Although minimizing *SST* largely solves the problem of estimation for the nonlinear least squares catch-at-age model, some loose ends still need to be tended. Doubleday (1976) realized early that at least one of the selectivities, usually the largest selectivity, needs to be made constant (i.e. fixed equal to 1.0). This is due to indeterminancy in the contribution of selectivity (s_j) and annual fishing mortality (F_i) to F_{ij}. If knife-edged recruitment is assumed, then all of the selectivities for ages greater than or equal to the age at recruitment will be set equal to 1.0. This process of fixing selectivities obviously reduces the number of parameters to be estimated in the model.

The next problem, that of estimating mean squared error, introduces some questions of how a sum of squares such as *SST* should be interpreted in light of standard statistical methods. Because λ in the *SST* expression is largely unknown, a standard interpretation of residuals might be misleading. This problem is important because the residual sum of squares is used to estimate mean squared error which is a component of the covariance matrix of parameter estimates from nonlinear least squares. Although this problem appears troublesome, model fitting results indicate that ignoring the problem (i.e. using MSE_1 below) does not severely bias the estimates of mean squared error in the application given below. However, this is probably not always the case.

I shall take the practical course of simply trying two different estimates of mean squared error. The first makes no adjustments to the nominal values, while the second makes every adjustment that appears reasonable. Assuming that the model is fit minimizing *SST*, there are two possible estimates of residual sums of squares: *SST*, and *SSC*, with corresponding estimates of the total number of observations: $m_1 = ya + b'$, where b' is the number of survey biomass estimates in *SSB*, and $m_2 = ya$ if *SSC* is used as an estimate of residual sum of squares. As for the number of parameters estimated, the nominal number is:

$$p_1 = 2a + 2y - 1 - \text{(the number of fixed } s_j\text{'s)}.$$

If we interpret each term in *SSB* as a constraint on the parameters, then

$$p_2 = 2a + 2y - b' - 1 - \text{(the number of fixed } s_j\text{'s)}.$$

The two estimates of mean squared error we use in this paper are then: $MSE_1 = SST/(m_1 - p_1)$ unadjusted, and $MSE_2 = SSC/(m_2 - p_2)$ adjusted. Note that $m_1 - p_1 = m_2 - p_2$ so that $MSE_2 < MSE_1$.

Estimating the Variance of Biomass

For reliability in the estimation process it is almost always desirable to estimate the log-parameters rather than parameters on the original scale. This can be seen to place all the parameters on a common scale, and probably reduces parameter-effects nonlinearity (Ratkowsky 1983). Consider the augmented vector of parameters estimated by minimizing *SST*. This vector includes the parameters that are estimated plus the parameters fixed to known constants:

$$\beta = \{\beta_k\} = \{\log(b_k)\}$$
$$= \{\log(F_1),\ldots,\log(F_y),\log(s_1),\ldots,\log(s_a),$$
$$\log(N_{11}),\ldots,\log(N_{1a}),\log(N_{21}),\ldots,\log(N_{y1})\}$$

The parameter estimates on the original scale are simply $b = \{b_k\} = \{\exp(\beta_k)\}$. The covariance matrix $S(\beta)$ is estimated using standard nonlinear least squares methods, and either MSE_1 or MSE_2. For parameters that were fixed, all variances and covariances are set equal to zero. Applying the delta method (Seber 1973), the covariance matrix of parameters on the original scale is simply $S(b) = \{b_i b_j \operatorname{cov}(\beta_i,\beta_j)\}$.

Recall the formulas for total and fishable biomass described earlier: $\hat{B}_i = \Sigma_j N_{ij} w_j$ and $\hat{B}_i^f = \Sigma_j N_{ij} s_j w_j$. To estimate the variance of these quantities in year i, we need the covariance matrix of

$$Y_i = \{N_{i1},\ldots,N_{ia},s_1,\ldots,s_a\}.$$

These can be estimated from $S(b)$, again using the delta method. Note that $N_{ij} = b_k$ for some k, if N_{ij} is a parameter in $b = \{b_k\}$. Otherwise, $N_{ij} = N_{i'j'} \exp\left[-\sum_{k=0}^{[i-i'-1]} (M + F_{i'+k} s_{j'+k})\right]$ where $N_{i'j'}$ is a parameter in b.

Define row vectors of length p:

$$\delta(N_{ij}) = \{\partial(N_{ij})/\partial(b_k)\}$$

and $\delta(s_j) = 1.0$ in the position s_j occurs in the vector b
0.0 elsewhere.

By the delta method, the elements of the covariance matrix $S(Y_i)$ can be estimated by

$$\operatorname{cov}(N_{ij},N_{ij'}) = \delta(N_{ij})\, S(b)\, \delta(N_{ij'})'$$
$$\operatorname{cov}(s_j,s_{j'}) = \delta(s_j)\, S(b)\, \delta(s_{j'})'$$

and $\operatorname{cov}(N_{ij}, s_{j'}) = \delta(N_{ij})\, S(b)\, \delta(s_{j'})'$.

Next define row vectors of length $2a$:

$$\delta(B_i) = \{w_1,..,w_a,0,\ldots,0\}$$

and $\delta(B_i^f) = \{s_1 w_1,\ldots,s_a w_a,N_{i1} w_1, \ldots,N_{ia} w_a\}$.

And finally, again by the delta method,

$$\operatorname{var}(\hat{B}_i) = \delta(B_i)\, S(Y_i)\, \delta\,(B_i)'$$

and $\operatorname{var}(\hat{B}_i^f) = \delta(B_i^f)\, S(Y_i)\, \delta(B_i^f)'$.

Tuning the Model Fit

In the model described above, tuning is a matter of determining what the value of λ should be, and then deciding what constraints should be placed on the selectivities. Because the mean squared error of $\log(c_{ij})$ is largely independent of assumptions concerning selectivities, the two problems can be considered independently.

First let us consider the problem of determining λ. As noted earlier, the theoretically optimal value is

$$\lambda = \operatorname{var}[\log(c_{ij})]/\operatorname{var}[\log(S_i^f)].$$

Assuming the catch-at-age model has no process error,

TABLE 1. Catch in numbers-at-age (millions) of walleye pollock from the Eastern Bering Sea. Average weight-at-age (kilograms) that were used are shown at the bottom.

	Age (yr)							
Year	2	3	4	5	6	7	8	9
1964	6.5	27.1	42.5	49.7	24.5	68.9	31.0	6.5
1965	4.9	5.3	70.6	190.3	46.6	11.6	11.2	5.3
1966	11.3	66.9	22.8	167.0	105.3	9.6	10.5	4.1
1967	8.0	93.1	488.0	74.1	135.2	32.1	9.7	4.8
1968	36.2	196.3	154.1	514.9	118.0	33.6	40.2	5.7
1969	19.1	103.8	597.6	410.8	141.1	3.0	15.8	10.1
1970	287.0	436.0	685.2	323.5	62.7	20.4	10.2	5.8
1971	444.0	132.6	740.7	497.2	737.1	71.6	47.0	13.2
1972	63.5	306.3	706.6	565.9	237.1	93.0	35.3	12.8
1973	652.0	730.8	1904.0	999.3	473.4	262.4	229.0	87.2
1974	3121.5	1403.0	421.1	484.4	248.4	156.9	128.0	133.7
1975	833.7	3817.1	458.9	53.7	84.1	95.6	70.1	53.4
1976	884.6	1618.9	1355.2	128.8	47.7	55.6	57.2	38.3
1977	1073.8	1195.8	847.5	274.6	75.0	32.1	46.0	41.2
1978	722.7	1097.4	944.4	391.3	94.4	26.3	17.7	19.1
1979	958.3	1235.4	682.5	541.0	231.8	53.8	22.8	29.2
1980	1120.1	1041.5	430.2	228.5	153.1	75.2	51.4	21.1
1981	76.5	1442.7	662.9	149.7	74.7	45.4	38.0	23.3
1982	25.4	214.9	1466.5	389.1	62.7	21.2	24.0	14.9
1983	96.2	187.2	430.0	912.1	207.8	33.0	13.3	9.1
1984	69.3	128.0	450.0	419.6	533.9	117.4	36.8	25.2
1985	119.4	546.6	174.6	384.1	370.7	510.7	137.7	47.9
Weight	0.105	0.251	0.409	0.565	0.650	0.798	0.892	0.945

TABLE 2. Estimates of fishable biomass (in million tons) from combined hydroacoustic and bottom trawl surveys. Estimates of cv(survey biomass) were approximated by estimating the standard deviation as the width of the 95% confidence interval divided by four.

Year	Biomass	Coefficient of variation
1979	10.5	0.148
1982	7.8	0.077
1985	9.4	0.085

TABLE 3. Biomass estimates (in million tons) from fitting the Doubleday–Deriso catch-at-age model assuming age 5-yr is fully available (i.e. $s_5 = 1$, and all other selectivities are estimated from the data), and $\lambda_0 = 10$. Estimates of cv are based on variance estimates using MSE_1, and estimates of adjusted cv are based on variance estimates using MSE_2 (see text).

	Total			Fishable		
Year	Biomass	cv	cv (adjusted)	Biomass	cv	cv (adjusted)
1964	25.183	0.934	0.898	14.323	0.830	0.798
1965	22.027	0.869	0.835	12.721	0.763	0.734
1966	17.841	0.775	0.745	10.012	0.691	0.665
1967	15.720	0.669	0.643	8.555	0.617	0.593
1968	15.699	0.594	0.571	9.020	0.550	0.529
1969	15.466	0.530	0.509	9.589	0.492	0.473
1970	14.632	0.443	0.426	9.565	0.427	0.410
1971	14.280	0.382	0.367	9.354	0.368	0.354
1972	13.393	0.366	0.352	8.570	0.324	0.311
1973	11.844	0.331	0.318	7.583	0.278	0.267
1974	9.571	0.340	0.327	4.999	0.296	0.285
1975	9.126	0.303	0.292	4.685	0.316	0.304
1976	10.296	0.259	0.249	6.390	0.298	0.286
1977	10.981	0.238	0.228	7.766	0.265	0.255
1978	11.041	0.228	0.219	7.985	0.233	0.224
1979	12.083	0.217	0.209	7.953	0.202	0.194
1980	14.672	0.207	0.199	8.341	0.202	0.194
1981	16.744	0.203	0.195	10.873	0.185	0.178
1982	17.228	0.199	0.191	13.292	0.169	0.162
1983	16.341	0.199	0.191	12.544	0.170	0.163
1984	14.537	0.203	0.195	9.353	0.181	0.174
1985	12.698	0.223	0.215	6.669	0.217	0.208

$$E(MSE) \approx \text{var}[\log(c_{ij})],$$

so that if we have some notion of $\text{var}[\log(S_i^f)]$, λ can be estimated. Note that depending on how the model is constrained an estimate of $\text{var}[\log(c_{ij})]$ based on *SSC* rather than *SST* may be appropriate. If *MSE* is not strongly influenced either by the trial value of λ, or the constraint on selectivities, a value for λ can be easily determined.

A more intuitive interpretation of λ is possible, since by the delta method $\text{var}[\log(X)] \approx \text{var}(X)/X^2$, so that $\text{var}[\log(X)]$ is roughly the squared coefficient of variation of X. Therefore,

$$\lambda \approx [\text{cv}(c_{ij})/\text{cv}(S_i^f)]^2.$$

This interpretation of λ is supported by the nonlinear least squares estimates of the coefficient of variation of fishable biomass,

$$\text{cv}(\hat{B}_i^f) = \text{sqrt}[\text{var}(\hat{B}_i^f)]/\hat{B}_i^f.$$

That is, if we fit the catch-at-age model using some value λ_o, the estimated $\text{cv}(B_i^f)$ is consistent with λ_o and the estimated value of *MSE*.

To elaborate, if the model is fit and $\text{cv}(\hat{B}_i^f)$ is estimated from the analytic estimates of variance, this value is roughly similar to the coefficient of variation of fishable biomass estimated from the above formula for λ (i.e. $\text{cv}(S_i^f) \approx \text{sqrt}(MSE/\lambda_o)$, remembering $MSE \approx \text{cv}(c_{ij})^2$). Such an interpretation seems possible only when the $\{S_i^f\}$ are assumed to be absolute estimates of fishable biomass rather than relative indices.

The other aspect of tuning I want to consider is that of constraining selectivities. It has already been pointed out that at least one s_j must be constrained to be equal to 1.0; the other selectivities may be estimated. However, if an age at full recruitment is assumed, all of the selectivities for ages greater than the age at full recruitment must be constrained to equal

TABLE 4. Estimates as in Table 3 except $\lambda_0 = 100$.

	Total			Fishable		
Year	Biomass	cv	cv (adjusted)	Biomass	cv	cv (adjusted)
1964	23.214	0.789	0.761	13.094	0.694	0.669
1965	20.463	0.732	0.706	11.780	0.642	0.619
1966	16.748	0.651	0.628	9.511	0.583	0.562
1967	15.007	0.562	0.542	8.144	0.518	0.500
1968	15.210	0.499	0.481	8.659	0.462	0.445
1969	15.195	0.445	0.429	9.342	0.414	0.399
1970	14.628	0.374	0.361	9.488	0.360	0.348
1971	14.449	0.324	0.313	9.439	0.313	0.302
1972	13.624	0.312	0.301	8.725	0.278	0.268
1973	12.104	0.284	0.274	7.764	0.245	0.237
1974	9.839	0.286	0.276	5.150	0.251	0.242
1975	9.620	0.250	0.241	4.802	0.258	0.249
1976	11.447	0.198	0.191	6.695	0.235	0.227
1977	12.833	0.165	0.160	8.757	0.181	0.175
1978	13.119	0.148	0.143	9.617	0.121	0.117
1979	13.403	0.146	0.141	9.476	0.077	0.074
1980	13.353	0.164	0.158	8.213	0.107	0.103
1981	13.819	0.164	0.158	8.464	0.096	0.093
1982	14.322	0.157	0.152	9.394	0.074	0.071
1983	14.320	0.156	0.150	9.756	0.092	0.089
1984	14.376	0.146	0.141	9.134	0.104	0.100
1985	13.949	0.162	0.156	8.564	0.079	0.076

TABLE 5. Estimates as in Table 3 except $s_j = 1$ for all $j \geq 4$.

	Total			Fishable		
Year	Biomass	cv	cv (adjusted)	Biomass	cv	cv (adjusted)
1964	2.310	0.261	0.250	1.981	0.285	0.272
1965	2.451	0.247	0.236	2.045	0.275	0.263
1966	2.668	0.218	0.209	2.006	0.258	0.247
1967	3.290	0.188	0.180	2.344	0.228	0.218
1968	4.154	0.172	0.165	2.896	0.208	0.199
1969	4.984	0.163	0.155	3.647	0.193	0.185
1970	6.008	0.152	0.145	4.479	0.174	0.167
1971	6.860	0.151	0.144	5.238	0.166	0.158
1972	6.702	0.163	0.156	5.516	0.173	0.165
1973	6.476	0.165	0.158	5.626	0.181	0.173
1974	5.112	0.144	0.138	3.410	0.169	0.162
1975	5.292	0.155	0.148	2.976	0.165	0.158
1976	6.333	0.154	0.147	4.232	0.180	0.172
1977	6.685	0.144	0.138	4.888	0.169	0.161
1978	6.573	0.135	0.129	4.984	0.156	0.149
1979	7.477	0.137	0.131	5.226	0.149	0.142
1980	9.816	0.141	0.135	5.743	0.172	0.164
1981	11.977	0.152	0.145	8.231	0.174	0.167
1982	13.216	0.159	0.152	11.462	0.166	0.158
1983	13.384	0.166	0.159	12.067	0.169	0.161
1984	12.976	0.181	0.173	11.461	0.177	0.169
1985	12.553	0.222	0.213	10.775	0.197	0.188

TABLE 6. Estimates as in Table 5 except $\lambda_o = 100$.

	Total			Fishable		
Year	Biomass	cv	cv (adjusted)	Biomass	cv	cv (adjusted)
1964	2.450	0.295	0.282	2.154	0.319	0.305
1965	2.584	0.278	0.266	2.188	0.307	0.294
1966	2.786	0.246	0.235	2.173	0.287	0.275
1967	3.399	0.212	0.203	2.503	0.254	0.243
1968	4.259	0.193	0.184	3.106	0.232	0.222
1969	5.061	0.181	0.173	3.842	0.214	0.205
1970	6.053	0.166	0.159	4.662	0.192	0.184
1971	6.876	0.163	0.156	5.415	0.181	0.173
1972	6.686	0.175	0.168	5.682	0.186	0.178
1973	6.374	0.178	0.170	5.653	0.193	0.185
1974	5.258	0.154	0.147	3.508	0.181	0.173
1975	5.958	0.163	0.156	3.435	0.192	0.183
1976	7.876	0.146	0.140	5.168	0.185	0.177
1977	9.297	0.116	0.111	6.690	0.154	0.147
1978	9.723	0.088	0.084	7.783	0.111	0.106
1979	9.960	0.078	0.075	8.354	0.078	0.074
1980	9.162	0.093	0.089	6.507	0.137	0.132
1981	9.761	0.075	0.072	7.220	0.116	0.111
1982	10.528	0.073	0.070	9.057	0.076	0.073
1983	10.815	0.077	0.074	9.599	0.080	0.077
1984	10.697	0.077	0.074	9.283	0.085	0.081
1985	10.254	0.115	0.110	8.952	0.080	0.077

1.0. A model assuming many fixed selectivities has fewer parameters and is therefore more stable (i.e. the estimated $\text{cv}(\hat{B}_i^f)$ are smaller). However, if the assumed pattern of fixed selectivities is incorrect the estimated parameters will be biased. I used the approximate F-test for nonlinear models (Draper and Smith 1966) to test the hypothesis that selectivities can be fixed.

Simulating the Catch-at-Age Model

Monte Carlo simulation is often used for model validation, the process by which we can to some extent confirm that the analysis based on a particular model and data set is providing meaningful results. In the present context validation would mean the following:

(1) Fit the model using real data and constraints.

(2) Take the estimated parameters as the "actual" model parameters for the simulation. This implies the simulation model fits the simulated data perfectly except for random error.

(3) Based on these parameters the "exact" catch-at-age data can be calculated. Assuming a particular $\text{cv}(c_{ij})$ for the catch-at-age data, which could be based on an observed *MSE* or any hypothetical value, simulate a new set of catch-at-age data with lognormal error.

(4) Using the same value of λ_o as was used to fit the real data, calculate a variance term for the "survey" estimates of fishable biomass (see discussion given below for derivation):

$$\text{cv}(S_i^f) = \text{sqrt}(\exp\{\text{var}[\log(c_{ij})]/\lambda_o\} - 1)$$
$$= \text{sqrt}(\exp\{\log[\text{cv}(c_{ij})^2 + 1]/\lambda_o\} - 1).$$

Use the computed fishable biomass from the model as the survey biomass before including the error term.

(5) Estimate the model parameters for the simulated data using the same constraints used in the original model fit.

If the resulting parameter estimates are reasonable estimates of the "actual" parameters then the model is to some extent validated. In their book *Numerical Recipes*, Press et al. (1986) refer to this method of inferring confidence in parameter estimates in its most general sense as "the only game in town."

Because the Doubleday–Deriso model assumes the $\log(c_{ij})$ are distributed as independent, normally distributed random variables, a minor dilemma arises concerning how the c_{ij} variates should be modelled. Denote the random variate based on c_{ij} as c^*_{ij}. If we choose that $E(c^*_{ij}) = c_{ij}$, then $E(\log(c^*_{ij})) \neq \log(c_{ij})$, and vice versa. I prefer satisfying the first equation, i.e. having unbiased catches on the original scale. From properties of the lognormal distribution (Finney 1941), it is easy to verify that if

$$\eta = \log[c_{ij}/\text{sqrt}(\text{cv}^2 + 1)], \text{ and}$$
$$\sigma = \text{sqrt}[\log(\text{cv}^2 + 1)],$$

then $X = \exp(\eta + \epsilon\sigma)$, where $\epsilon \sim N(0,1)$, is distributed as a lognormal random deviate with mean c_{ij} and coefficient of variation cv. If we want the catches to be unbiased on the logarithmic scale, simply substitute $\eta_1 = \log(c_{ij})$ for η. Trying it both ways seems not to make much difference.

Furthermore, the approximation

$$E(MSE) \approx \sigma^2$$
$$\approx \log(\text{cv}^2 + 1)$$

should hold, so that

$$\text{cv} \approx \text{sqrt}[\exp(MSE) - 1].$$

Application

The preceding analysis was applied to the walleye pollock (*Theragra chalcogramma*) fishery in the Eastern Bering Sea, which over the past 20 yr has averaged landings of over 1 000 000 t annually. I used catch-at-age data from commercial fishing operations (Table 1), and survey estimates of fishable biomass from combined trawl and hydroacoustic surveys in 1979, 1982, and 1985 (Table 2). These surveys were the most thorough, including midwater, shelf bottom, and slope bottom components. We interpret these surveys as estimates of fishable, rather than total biomass, because a significant number of older fish are now believed to migrate to the Bering Sea basin, where they have only recently been exposed to harvest. The annual natural mortality rate was assumed to be $M = 0.3$, and the average weight-at-age data are shown in Table 1.

For model fitting I considered two values of λ, $\lambda_o = 10$ and $\lambda_o = 100$. The values of λ considered for this analysis were based on the theory we have developed concerning the meaning of λ. An MSE_1 of 0.5 (Table 7) corresponds to

$$\text{cv}(c_{ij}) = \text{sqrt}[\exp(0.5) - 1.0] = 0.8.$$

A value of λ_o then implies that $\text{cv}(B_i^f) = \text{sqrt}(0.5/\lambda_o)$. For $\lambda_o = 10$, this means $\text{cv}(B_i^f) = 0.22$, and for $\lambda_o = 100$, $\text{cv}(B_i^f) = 0.07$. These values are roughly confirmed in Table 3, 4, 5, and 6. Because these values encompass the most probable range of $\text{cv}(B_i^f)$ (Table 2), they were assumed to be adequate limits for this analysis.

I also considered two possibilities for selectivities. The first possibility is that selectivities are estimated (but with s_5 fixed equal to 1). The second possibility is that of full recruitment at age 4 yr and older (i.e. $s_j = 1, j \geq 4$). Note that this is not strict knife-edged selectivity because s_2 and s_3 are allowed to be estimated from the data. For convenience I call the first assumption "estimated selectivities" and the latter "fixed selectivities."

For the model fits corresponding to these four assumptions concerning selectivities and λ, Fig. 1 shows the residuals of log(catch). The residuals appear reasonably normal; however, a slight bias appears in the residuals for the fixed selectivities model. The estimated biomasses from these model fits (Tables 3, 4, 5, and 6) are graphed in Fig. 2. From these four model

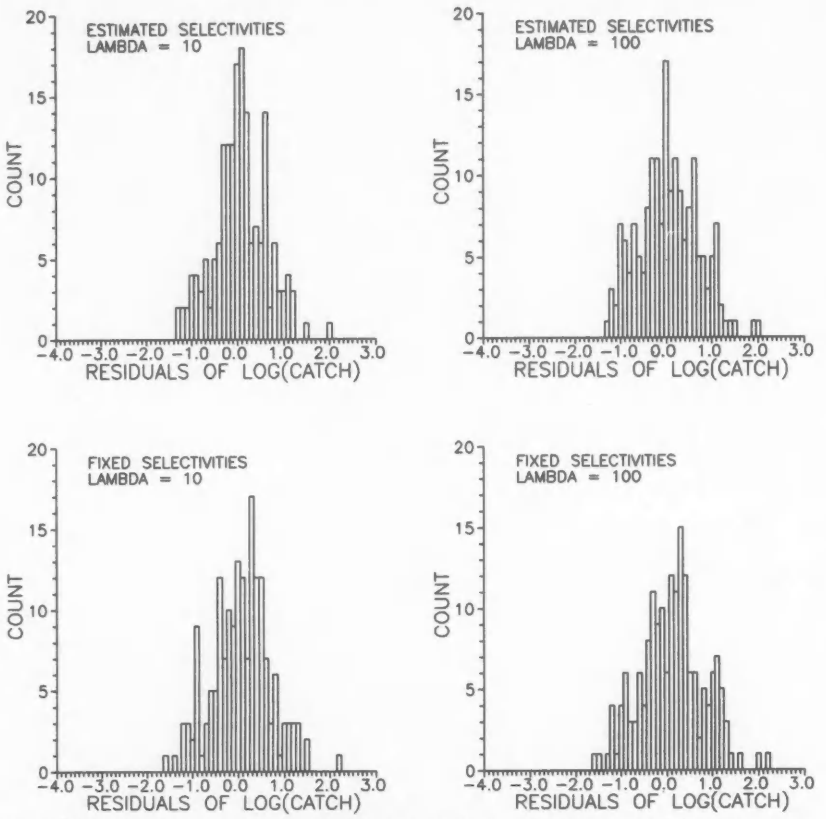

FIG. 1. Estimates of residuals on the logarithmic scale for four model fits to the Doubleday–Deriso catch-at-age model. Top two figures are from fits to the estimated selectivities model, bottom two figures are from fits to the fixed selectivities model.

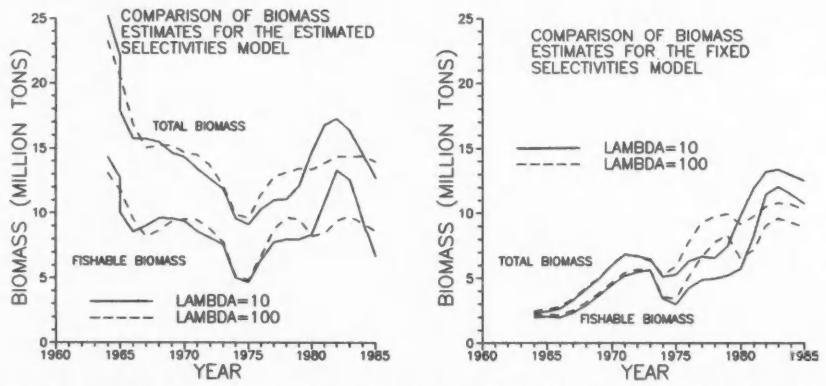

FIG. 2. Graph of estimated biomasses for four model fits to the Doubleday–Deriso catch-at-age model. Left graph is from fits to the estimated selectivities model, right graph is from fits to the fixed selectivities model.

fits three conclusions appear obvious. First there is a strong relative bias between the estimated and fixed selectivities models; second, for the same value of λ, the fixed selectivities model results appear to have much smaller variability; and finally, the larger λ is, the smaller the coefficient of variation of biomass estimates in years close to when the surveys were held.

None of these findings is surprising. The assumption of fixed selectivities is very strong and reduces variability in the results because fewer critical selectivity parameters have to be estimated. However, if this assumption is incorrect the results will be biased. In this problem we see the classic statistical trade

TABLE 7. Analysis of variance for testing the hypothesis of fixed selectivities for walleye pollock in the Eastern Bering Sea. Independent analyses are provided in two columns assuming $\lambda_0 = 10$ and $\lambda_0 = 100$. Regardless of how the F-statistic is calculated, the hypothesis of fixed selectivities is rejected at the $\alpha = 0.001$ level.

Source	$\lambda_0 = 10$	$\lambda_0 = 100$
(1) Residuals assuming $s_5 = 1$	63.369	77.151
(2) Residuals assuming $s_j = 1, j \geq 4$	76.947	91.888
(3) $SS_H = (2) - (1)$ above	13.578	14.737
(4) $MS_H = SS_H/5.0$	2.716	2.947
(5) MSE_1 described in text assuming $s_5 = 1$	0.524	0.638
(6) $F(5,121) = MS_H/MSE_1$	5.18	4.62

Age (yr)	Estimated Selectivities $\lambda_0 = 10$ Estimated	$\lambda_0 = 10$ Fixed	$\lambda_0 = 100$ Estimated	$\lambda_0 = 100$ Fixed
2	0.164	0.121	0.151	0.129
3	0.568	0.438	0.552	0.531
4	0.989	1.000	0.940	1.000
5	1.000	1.000	1.000	1.000
6	0.718	1.000	0.759	1.000
7	0.349	1.000	0.356	1.000
8	0.338	1.000	0.333	1.000
9	0.242	1.000	0.238	1.000

off between bias and variance. Also, increases in λ force the biomass estimates through the survey results which will obviously reduce variance.

As suggested earlier, it is possible to use residuals to test hypotheses concerning fixed selectivities. This has been done using the extra sum of squares principle (Draper and Smith 1966), with the results displayed in Table 7. It appears clear that the hypothesis of fixed selectivities (i.e. $s_j = 1, j \geq 4$) can be rejected at the $\alpha = 0.001$ level. Therefore, we conclude the analysis with selectivities estimated (Table 3 and 4, Fig. 2) is the more relevant for walleye pollock in the Eastern Bering Sea.

Having narrowed the analysis to the model in which selectivities are estimated, we have only to choose between $\lambda_0 = 10$ and $\lambda_0 = 100$. Figure 2 shows that the fit for these models differ only during recent years when the survey biomass estimates were available. The fit with $\lambda_0 = 100$ constrains the model to the surveyed values while $\lambda_0 = 10$ allows the model latitude for variability. The choice is really one of believing the trend in the surveys or the trend in the age data. The estimates of $cv(S_i^f)$ calculated from the surveys (Table 2) would favor $\lambda_0 = 100$, but my feeling is that these cv's underestimate the level of uncertainty.

An attempt was made to fit the model assuming that the survey biomass estimates were relative rather than absolute estimates of abundance. For the pollock data set, such auxiliary information was insufficient to adequately constrain the model (i.e. the coefficients of variation of biomass estimates were too large). If surveyed biomasses are relative indices rather than absolute estimates (i.e. if q is unknown) the ability of survey data to constrain the model is greatly reduced.

In an attempt to validate the analysis, a Monte Carlo simulation of the model was performed assuming selectivities were estimated and $\lambda_0 = 10$. As described earlier an *MSE* of 0.5 (Table 7) implies that $cv(c_{ij}) = 0.8$, and further assuming $\lambda_0 = 10$, implies $cv(S_i^f) = 0.22$. These coefficients of variation were used to generate the lognormal error terms. The simulations had 30 replications with the results shown in Fig. 3 and 4. In these figures the "actual" biomass estimates and "analytic" coefficient of variation estimates are based on the model fit, with variability estimated from the nonlinear least squares analysis (Table 3).

The main result of the simulation is that biomass estimates in the early years appear severely biased high (Fig. 3). This bias cannot be due to process error because the simulations were performed in such a way that there is no process error. The most obvious reason for this bias is that the model is simply not sufficiently constrained for the earlier years, considering the high level of residual error in the catch-at-age data. The estimates of the coefficients of variation for the biomass estimates (Fig. 4) appear reasonable considering the approximate nature of the delta method which was used extensively.

The simulation results show that even if a model is known to describe the population dynamics exactly, the modelling results may still be significantly biased. Ratkowsky (1983) points out that Box's (1971) estimate of bias is proportional to variance, so it is not surprising to see bias when error variance is as large as in our example. If $cv(c_{ij})$ is reduced to 0.25, bias becomes much smaller (Fig. 5).

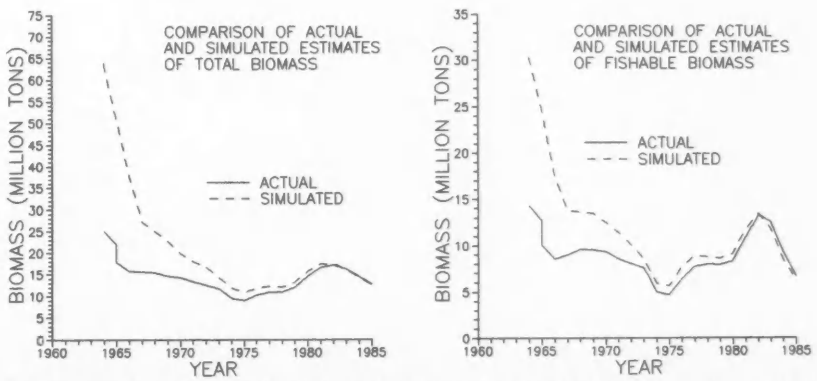

FIG. 3. Comparison of "actual" and simulated estimates of total and fishable biomass from a Monte Carlo simulation ($N = 30$) that estimated selectivities from the data, and assumed $\lambda_0 = 10$. Actual results are from Table 3.

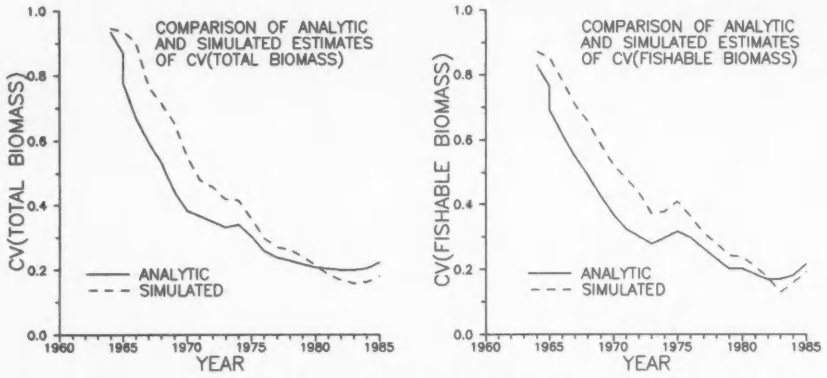

FIG. 4. Comparison of analytic (i.e. delta method) and simulated estimates of the coefficient of variation of total and fishable biomass estimated from a Monte Carlo simulation ($N = 30$) that estimated selectivities from the data, and assumed $\lambda_o = 10$. Analytic results are from Table 3.

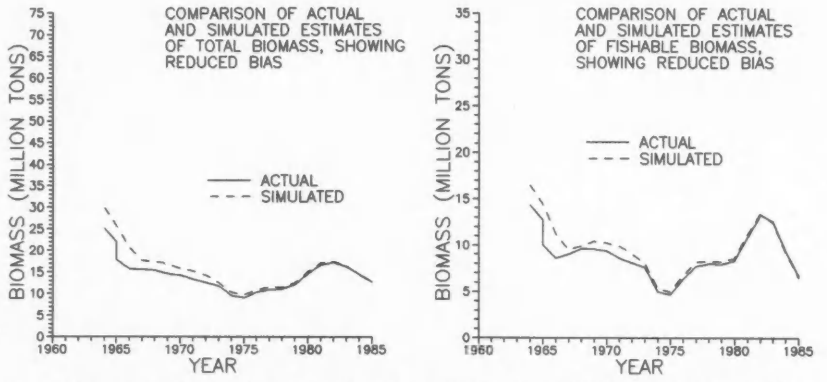

FIG. 5. Comparison of "actual" and simulated estimates of total and fishable biomass from a Monte Carlo simulation ($N = 30$) when $cv(c_{ij})$ is reduced to 0.25. We also assume that selectivities are estimated from the the data, and that $\lambda_o = 10$. Actual results are from Table 3.

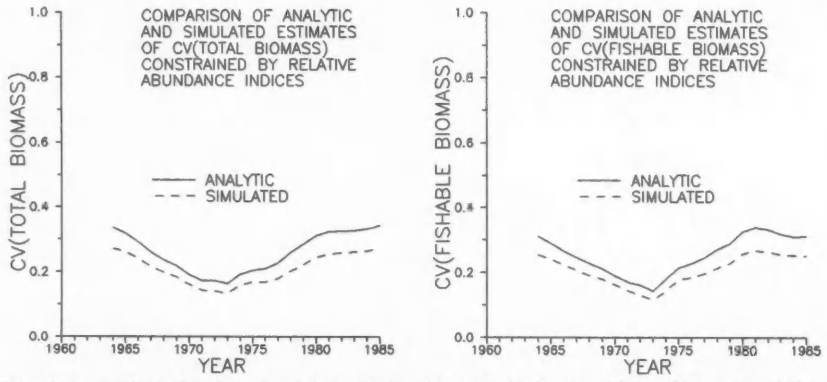

FIG. 6. Comparison of analytic (i.e. delta method) and simulated estimates of the coefficient of variation of total and fishable biomass when survey relative abundance indices are known for the first and last years of catch data. The coefficient of variation of catch-at-age was assumed to be a low $cv(c_{ij}) = 0.1$, and $\lambda_o = 10$.

For the sole purpose of further testing the analytic (delta method) estimates of variability with Monte Carlo simulation estimates, I assumed the model fit in Table 3, that surveyed indices were available for the first and final years of catch data, that $\lambda_o = 10$, and that the coefficient of variation of the catch data was a low value (i.e. $cv(c_{ij}) = 0.1$). The results (Fig. 6)

support the conclusion that the analytic estimates of variance of total and fishable biomass are approximately correct. Note, however, that the $cv(c_{ij})$ is much smaller than $cv(\hat{B}_i^f)$.

Discussion

The Doubleday–Deriso model brings new insight into the analysis of catch-at-age data. Perhaps for the first time, constraints can be applied systematically, and overall variability in the model assessed. This does not mean that we will always like what we see. Catch-at-age data often contains a great deal of residual error, and this error must be reflected in uncertainty in modelling results.

Without the addition of strong assumptions (e.g. stock–recruitment relationships, or effort data), year-class strengths, and annual fishing mortality rates are based on at most a observations. Selectivities are based on y observations, but are often known to change with time. Therefore, unlike most applications of nonlinear least squares, we do not have statistical consistency (i.e. the parameter estimates do not converge to their correct values as sample size increases). If we do make the additional assumptions required to reduce the variability in modelling results, we run the risk of introducing significant bias as was seen in the introduction of fixed selectivities in our example.

Explaining bias in a model as complicated as the Doubleday–Deriso model is not easy. That is one of the reasons why bootstrapping and simulation are such important tools; bias and variance can be explored much more easily computationally than theoretically. As pointed out so well by Ratkowsky (1983) bias and variance are a function of both the model and data, and in our case the auxiliary information and how this information is used. Even the dramatic bias between biomass estimates from the estimated selectivities and fixed selectivities model (Fig. 2) can not be easily explained. If true selectivities are less than 1.0, and selectivities are assumed to be 1.0, it is easy to understand that total biomass would be underestimated. But explaining why this bias increases going backwards in time is more difficult.

Some researchers may think the results showing increasing variance in the biomass estimates calculated for earlier years contradicts Pope's (1972) paper on the convergence of cohort analysis. Pope's (1972) result is sometimes paraphrased as meaning that the results from cohort analysis are more reliable for earlier years than for later years, given that the model is constrained in the most recent years. I am uncomfortable with this interpretation. Pope's (1972) original paper dealt with just a single cohort, and showed that the estimated numbers-at-age have decreasing percentage error as one moves to younger ages, regardless of the terminal F_t that is chosen. In a real catch-at-age analysis we are dealing with several cohorts, and the biomass estimates contain all ages. In fact, the older ages in the earliest years of any catch-at-age analysis can be based on only a few year's catches. Unless constraints can be placed on the model in earlier years, I am more comfortable with the notion that variability (i.e. uncertainty) increases as we go backwards in time.

Finally, the application of the model concerning pollock in the Eastern Bering Sea should be interpreted only as an example. Assessing the Bering Sea pollock stocks is a very complex problem, and I do not wish to second guess those charged with that task.

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Effects of Temperature on the Oxidation of Fatty Acids, Acyl Carnitines, and Ketone Bodies by Mitochondria Isolated from the Liver of the Lake Charr, *Salvelinus namaycush*

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Mitochondria isolated from the liver of the Lake Charr *Salvelinus namaycush* oxidize a wide range of acyl chain lengths of fatty acids and acyl carnitines at 1, 10, and 20°C. For most carbon chain lengths the relative importance of carnitine-dependent fatty acid oxidation increases with increasing temperature due to greater thermal enhancement of carnitine-dependent oxidation. At low temperatures the rate of carnitine-independent fatty acid oxidation rivals that of carnitine-dependent oxidation. Therefore, acute temperature shifts during excursions above the thermocline would have important effects on the oxidation of dietary and depot lipids. Temperature does not substantially affect the chain length preference for fatty acid oxidation either in the presence or absence of carnitine, suggesting acclimation-induced changes in substrate specificity of fatty acid oxidation may not be necessary. The importance of β-hydroxybutyrate as an oxidative substrate increases at low temperatures relative to other substrates while acetoacetate oxidation is greater than that of β-hydroxybutyrate at 10 and 20°C. Altered ketone body metabolism may play a role in regulating cholesterol levels to alter membrane fluidity.

Les mitochondries isolées du foie du touladi *Salvelinus namaycush* oxydent des acides gras et des acyl-carnitines de différentes longueurs de chaîne à 1, 10, et 20°C. Pour presque toutes les longueurs de chaîne du carbone, l'importance relative de l'oxydation des acides gras dépendant de la carnitine augmente avec la hausse de la température à cause d'une augmentation thermique plus grande de l'oxydation dépendante de la carnitine. À basse température, le taux d'oxydation des acides gras dépendant de la carnitine rivalise avec celui de l'oxydation dépendante de la carnitine. Par conséquent, des changements marqués de température pendant des incursions au-dessus de la thermocline auraient des effets importants sur l'oxydation des lipides alimentaires et des lipides de dépôt. La température ne modifie pas de façon importante la préférence pour une longueur de chaîne pour l'oxydation des acides gras en présence ou en l'absence de carnitine ce qui porte à croire que les changements induits par l'acclimatation au niveau de la spécificité du substrat pour l'oxydation des acides gras peuvent ne pas être nécessaires. L'importance du β-hydroxybutyrate comme substrat d'oxydation augmente à basse température par rapport à d'autres substrats tandis que l'oxydation de l'acétoacétate est plus grande que celle du β-hydroxybutyrate à 10 et à 20°C. Le métabolisme modifié des corps cétoniques peut jouer un rôle au niveau de la régulation du taux de cholestérol pour modifier la fluidité des membranes.

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Lipid is a major energy store in most animal species. In mammals, after lipolysis, long-chain fatty acids from depot triglyceride must be esterified to *L*-carnitine to be transferred into the mitochondrial matrix where oxidation can occur (see Bremer 1983 for review). This transfer is thought to be rate limiting in the oxidation of long-chain fatty acids (McGarry and Foster 1980). Short-chain fatty acids do not require *L*-carnitine for oxidation. Our current understanding of the oxidation of lipid is based largely on studies of mammalian systems. The role of *L*-carnitine in long-chain fatty acid oxidation is not well established in fish and may be less important than in mammals.

The early studies of Brown and Tappel (1959) demonstrated the ability of carp liver mitochondria to oxidize long-chain fatty acids at comparable rates to rat liver mitochondria in the absence of carnitine. Bilinski and Jonas (1970) demonstrated a carnitine-dependent mechanism for fatty acid oxidation by a variety of rainbow trout (*Onchorynchus mykiss*) tissues. The mitochondrial oxidation of acyl carnitines of varying chain lengths and degrees of saturation has now been demonstrated in a variety of tissues of numerous fish species (see Henderson and Tocher (1987 for review). Based on the mammalian paradigm it is generally assumed that carnitine-dependent oxidation of medium and long-chain fatty acids is vastly more important than carnitine-independent fatty acid oxidation. The early studies of fish mitochondria did not use demonstrably intact mitochondrial systems and no recent studies have compared the importance of carnitine-independent and carnitine-dependent mechanisms in fish. Intact mitochondria are essential to esti-

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mations of the relative importance of carnitine-dependent versus independent fatty acid oxidation.

Due to the known effects of temperature on the fluidity and permeability of membranes, thermal changes may differentially affect the carnitine-dependent and independent movement of fatty acids into the mitochondrial matrix. In liver, partitioning of dietary and depot fatty acids between carnitine-dependent and carnitine-independent mechanisms at different temperatures may be an important adaptation to acute temperature change such as those occurring during brief excursions above the thermocline.

Ketone bodies do not appear to be important in the metabolism of starving teleost fish (Zammit and Newsholme 1979) but production of ketone bodies by cold-acclimated fish may provide precursors for cholesterol synthesis. Cholesterol plays an important role in determining membrane fluidity (Hazel 1984). Indeed, Teichert and Wodtke (1987) report elevated levels of the rate-limiting enzyme in cholesterol synthesis from ketone bodies, hydroxy-3-methylglutaryl CoA reductase, in cold-acclimated carp, and Jankowsky et al. (1984) report increased acetoacetate production by hepatocytes isolated from cold-acclimated eels. Regulation of ketone body metabolism may be a critical factor in dealing with low temperature stress.

We therefore examined the effects of temperature on the oxidation of ketone bodies and on the carnitine-independent and carnitine-dependent fatty acid oxidation by intact liver mitochondria. To provide the greatest low temperature challenge under physiological conditions, a cold water teleost which remains active at the lowest nonfreezing temperatures, the lake charr, *Salvelinus namaycush* (Crawshaw 1984) was chosen.

Materials and Methods

Animals

Lake charr of both sexes (600–1000 g) were obtained from a local supplier and maintained at the University of Guelph at 10 ± 2°C with a 12:12 photoperiod for 12 wk before the experiments. Fish were fed ad libitum a commercial salmon diet 84G, Martin Feed Mills Ltd., Elmira, Ontario.

Mitochondrial Isolation

Fish were stunned with a sharp blow to the head, the liver was rapidly removed and placed in ice cold isolation medium consisting of 250 mM sucrose, 1 mM EGTA (ethylene glycol bis-(β-aminoethyl ether) *N,N,N′,N′*-tetraacetic acid), 30 mM HEPES (*N*-2-hydroxyethylpiperazine-*N′*-2-ethanesulfonic acid) buffer pH 7.20 at 20°C, and 1% BSA, (bovine serum albumin, Sigma A-7030, essentially fatty acid free). The liver was rapidly minced and homogenized with three passes of a loosely fitting teflon pestle in a Potter–Elvehjem homogenizer. The homogenate was then centrifuged for 10 min at 500 × g. The resulting supernatant was removed and centrifuged for 10 min at 5700 × g. The pellet was removed, resuspended in the same medium and again centrifuged for 10 min at 5700 × g. The final pellet was resuspended in the isolation medium to give a final mitochondrial protein content of 2 $mg \cdot ml^{-1}$. This method yields mitochondria with respiratory control ratios (RCR's) of 6.83 with pyruvate as a substrate at 10°C in the medium described below.

Mitochondrial Respiration

Oxygen consumption was measured with a Clark-type electrode in 1-ml cells maintained at the appropriate temperature ± 0.1°C with a Haake water circulator. Three temperatures were chosen for the assays: the acclimation temperature (10°C); a low temperature close to the lower limit (freezing point of water) and a high temperature close to the upper lethal limit for this species (23.5°C; Gibson and Fry 1954). Mitochondria were incubated in a medium consisting of 150 mM KCl, 30 mM HEPES pH 7.20 at 20°C, 10 mM KH_2PO_4 and 1% BSA. One volume of mitochondrial suspension was added to nine volumes of reaction medium. The absence of significant endogenous respiration permitted ADP to be added initially with substrates being added after the addition of ADP. The stimulation of the rate of oxidation of NADH expressed as a percentage of the state 3 rate for glutamate was less than 2.5% at all temperatures indicating permeability of the mitochondria was not compromised at any of the temperatures used.

State 3 respiration was taken to be the rate in the presence of both ADP (200 μM) and substrate and state 4 the rate following state 4 due to depletion of ADP. Concentrations of substrates used were determined to be optimal at each temperature (butryric acid (C-4), caproic acid (C-6), caprylic acid (C-8) and capric acid (C-10), 200 μM at 1°C, 100 μM at 10°C, 100 μM at 20°C; lauric acid, 200μM at 1, 10, and 20°C; myristic and palmitic acids, 20 μM at 1°C, 50 μM at 10°C, 20 μM at 20°C; Stearic acid 10 μM at 1°C, 50 μM at 10°C, and 20 μM at 20°C: acetyl *DL*-carnitine, 100 μM at 1°C, 150 μM at 10°C, 100 μM at 20°C; hexanoyl *DL*-carnitine, 50 μM at 1°C, 150 μM at 10°C, 100 μM at 20°C; octanoyl *DL*-carnitine 100 μM at 1, 10, and 20°C; decanoyl *DL*-carnitine 50 μM at 1°C, 100 μM at 10°C, 50 μM at 20°C; lauroyl *DL*-carnitine, 100 μM at 1, 10, and 20°C; myristoyl *DL*-carnitine, 100 μM at 1°C, 50 μM at 10 and 20°C; palmitoyl *DL*-carnitine, 100 μM at 1°C, 50 μM at 10°C, 100 μM at 20°C; stearoyl *DL*-carnitine, 100 μM at 1 and 10°C, 50 μM at 20°C; 5 mM glutamate; 1 mM pyruvate; 1 mM

TABLE 1. Effects of temperature on respiratory control ratios for oxidation of glutamate and pyruvate by mitochondria isolated from the liver of *Salvelinus namaycush*. Values are means ± SE. Methods are as reported in materials and methods. Number of determinations are in parentheses.

Substrate	1°C	10°C	20°C
Glutamate	5.87 ± 0.52(8)	4.49 ± 0.49(9)	5.13 ± 0.35(9)
Pyruvate	6.58 ± 0.95(6)	6.83 ± 0.82(7)	5.42 ± 0.61(6)

TABLE 2. Q_{10} values for state 3 oxidation of substrates by mitochondria isolated from the liver of *Salvelinus namaycush*.

	Q_{10}			
Substrate	1–10°C		10–20°C	
Glutamate (5 mM)	3.11		2.06	
Pyruvate (1 mM)	4.76		1.61	
Acyl chain length	Fatty acid	Acyl carnitine	Fatty acid	Acyl carnitine
4	1.68	NA	1.76	NA
6	1.53	1.85	1.84	2.35
8	1.48	1.95	1.92	3.51
10	1.60	1.85	2.02	2.24
12	1.91	2.02	1.83	2.42
14	1.50	1.85	2.35	2.33
16	1.76	1.95	2.02	2.26
18	1.93	2.01	2.14	1.96

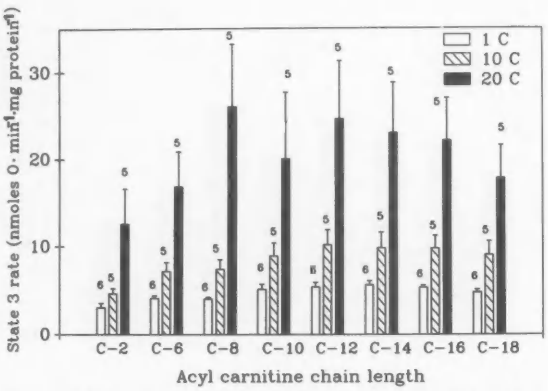

FIG. 1. Effects of temperature on the state 3 rate of oxidation of acyl carnitines of varying chain length by mitochondria isolated from the liver of the lake charr (*Salvelinus namaycush*). Conditions were as reported in materials and methods. The number of determinations is given above each bar. Values given are means ± SE.

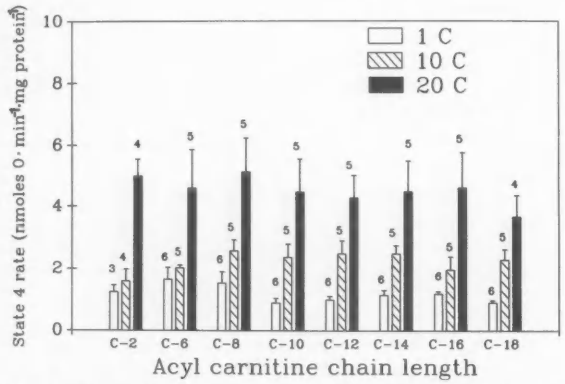

FIG. 2. Effects of temperature on the state 4 oxidation rate in the presence of acyl carnitines of varying chain length by mitochondria isolated from the liver of the lake charr (*Salvelinus namaycush*). Conditions were as reported in materials and methods. The number of determinations is given above each bar. Values given are means ± SE.

β-hydroxybutyrate; 1 mM acetoacetate). Malate (0.1 mM) was added to all fatty acid and acyl carnitine, glutamate and pyruvate determinations to provide "sparking" amounts of four carbon units. The possible contribution of peroxisomal fatty acid oxidation was ruled out by addition of sodium azide (10 mM) in state 3. The addition of azide eliminated the oxidation of fatty acids indicating no peroxisomal contamination. Respiratory control ratios were determined from the ratio of the state 3 rate to the state 4 rate. Mitochondrial protein was determined by the method of Gornall et al. (1949). The protein content of the isolation medium was determined and subtracted from the total protein to determine the mitochondrial protein.

Chemicals and Biochemicals

All chemicals and biochemicals were obtained from the Sigma Chemical Co., St. Louis, MO and were of the highest purity available.

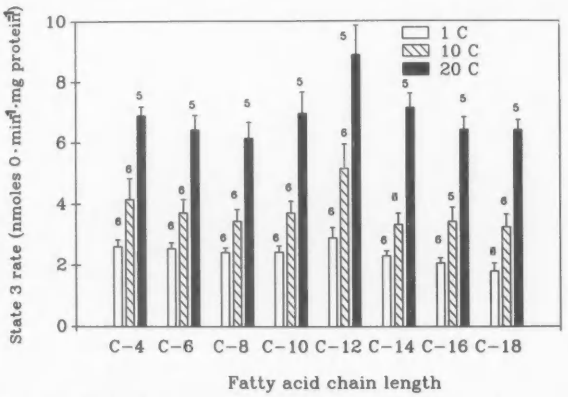

FIG. 3. Effects of temperature on the state 3 rate of oxidation of various fatty acids by mitochondria isolated from the liver of the lake charr (*Salvelinus namaycush*). Conditions were as reported in materials and methods. The number of determinations is given above each bar. Values given are means ± SE.

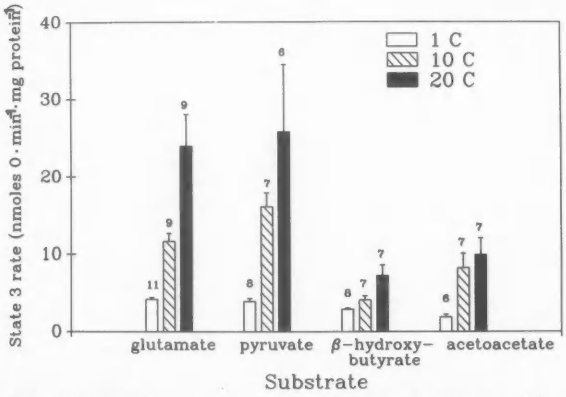

FIG. 4. Effects of temperature on the state 3 rate of oxidation of glutamate, pyruvate, acetoacetate, and β-hydroxybutyrate by mitochondria isolated from the liver of the lake charr (*Salvelinus namaycush*). Conditions were as reported in materials and methods. The number of determinations is given above each bar. Values given are means ± SE.

Statistical Analysis

Statistical comparisons were made using the Students *t*-test for unpaired samples.

Results

Temperature did not affect the quality of the mitochondria as judged from the RCR values for glutamate and pyruvate which did not differ significantly at any of the temperatures examined (Table 1).

The Q_{10} values calculated from mean state 3 rates are higher for glutamate and pyruvate over the range 1–10°C than for the range 10–20°C (Table 2). On the other hand the Q_{10} is lower for all acyl carnitines in the range 1–10°C compared with the range 10–20°C (Table 2). The Q_{10} values for fatty acid oxidation are lower over the range 10–20°C than those of the corresponding acyl carnitines (Table 2).

Increasing temperature increased the rate of oxidation of all substrates examined. There was little effect of temperature on

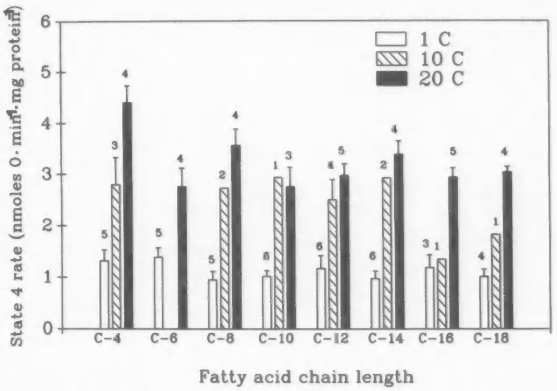

FIG. 5. Effects of temperature on the state 4 oxidation rate in the presence of various fatty acids by mitochondria isolated from the liver of the lake charr (*Salvelinus namaycush*). Conditions were as reported in materials and methods. The number of determinations is given above each bar. Values given are means ± SE.

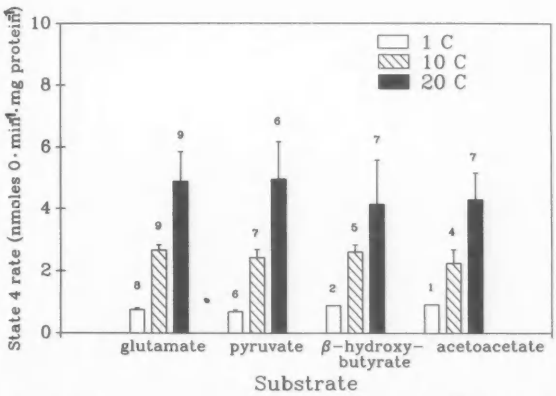

FIG. 6. Effects of temperature on the state 4 rate of oxidation in the presence of various substrates by mitochondria isolated from the liver of the lake charr (*Salvelinus namaycush*). Conditions were as reported in materials and methods. The number of determinations is given above each bar. Values given are means ± SE.

the preferred chain length of acyl carnitines oxidized in state 3 (Fig. 1) or state 4 (Fig. 2). Fatty acids were oxidized at rates about one half the rate of the comparable acyl carnitine at 20°C, slightly less than one half the rate of the comparable acyl carnitine at 10°C, but at rates approaching those of the comparable acyl carnitines at 1°C (Fig. 3).

β-hydroxybutyrate state 3 oxidation was about one-third that of glutamate at 10 and 20°C but rose to two-thirds that of glutamate at 1°C (Fig. 4). Acetoacetate state 3 oxidation was about 70% that of glutamate at 10°C but only 40% at 1 and 20°C. At 1°C β-hydroxybutyrate oxidation exceeded that of acetoacetate, but at 10 and 20°C acetoacetate oxidation was higher than that of β-hydroxybutyrate (Fig. 4).

State 4 rates of oxidation in the presence of fatty acids of various chain lengths were similar at each temperature (Fig. 5). Glutamate and pyruvate were oxidized at comparable rates to the perferred acyl carnitines at all temperatures (Fig. 4). State 4 rates of oxidation in the presence of glutamate, pyruvate, β-hydroxybutyrate and acetoacetate were similar at each temperature (Fig. 6).

Discussion

Oxidation of saturated acyl carnitines in trout liver mitochondria has broad chain-length specificity (Henderson and Sargent 1985). The acyl chain length preferences of lake charr are similar to those reported for liver mitochondria from other vertebrates (elasmobranch, Ballantyne and Moon 1986; avian, Ballantyne et al. 1988).

The increasing preference for acyl carnitines over fatty acids with increasing temperature is likely due to thermal enhancement of carnitine-dependent oxidation relative to carnitine-independent oxidation. The studies of Ramsay and Tubbs (1976) have shown that the transport of carnitine across the inner mitochondrial membrane of rat heart mitochondria has an unusually high Q_{10} (8.5) over the range 0–18°C. This suggests transport of acyl carnitines across the inner mitochondrial membrane would become increasingly limited at low temperatures. The present study indicates higher Q_{10} values for acyl carnitines over the range 10 to 20°C compared with 1–10°C. Higher Q_{10} values for acyl carnitines compared with the corresponding fatty acid indicate greater thermal enhancement of carnitine-dependent oxidation of fatty acids compared with carnitine-independent oxidation.

The studies of Murata (1979) and Murata and Higashi (1979) indicate free fatty acids are oxidized by isolated red muscle and liver mitochondria of several species of fish. Bilinski and Jonas (1970) showed differences in the ability of various rainbow trout tissues to oxidize fatty acids without carnitine. These studies provided no assessment of the integrity of the mitochondria used and cannot be employed to determine the in vivo importance of carnitine-independent fatty acid oxidation. The isolation medium used in the study of Bilinski and Jonas (1970) was markedly hyperosmotic while the incubation medium was hypoosmotic. Ballantyne and Moyes (1987) found that osmotic conditions influenced the chain length preference for the oxidation of acyl carnitines by mollusc mitochondria. Similar effects on teleost mitochondria could alter the relative importance of carnitine-independent fatty acid oxidation and substantially underestimate the physiological importance of this mechanism in fatty acid catabolism. The liver mitochondria from *Salvelinus namaycush* in the present study oxidized fatty acids at about one half the rate of the corresponding acyl carnitine at the acclimation temperature, while Bilinski and Jonas (1970) found (*Onchorynchus mykiss*) liver mitochondria oxidized fatty acids at only one-tenth the carnitine-dependent rate.

Carnitine-independent fatty acid oxidation may be physiologically important in the liver in the catabolism of dietary fatty acids from the intestine. Muscle mitochondria from lake charr do not oxidize fatty acids at detectable levels although acyl carnitines are oxidized at high rates (P. Blier and J. S. Ballantyne, unpubl. data). The effects of temperature on the mode of liver fatty acid oxidation could affect the catabolism of dietary lipids in lake charr during acute temperature shifts as occur during excursions above the thermocline (Scott and Crossman 1973).

Although depot lipid fatty acid composition changes with thermal acclimation (see Greene and Selivonchick 1987 for review) the present study indicates corresponding changes in the chain-length preference for oxidation of fatty acids in liver of lake charr by either carnitine-dependent or independent mechanisms may not require metabolic restructuring during

thermal acclimation due to the wide range of fatty acids and acyl carnitines accepted.

Oxidation of both acetoacetate and β-hydroxybutyrate indicate the liver may function in a ketogenic or ketolytic capacity and this may be modulated by acute temperature change. Ketone bodies are produced when the rate of β-oxidation exceeds the capacity of Krebs cycle to oxidize the acetyl CoA produced (see McGarry and Foster 1980 for review). Ketone bodies function as alternatives to carbohydrate derived carbon during periods of starvation in many vertebrates including elasmobranchs but not teleost fishes (Zammit and Newsholme 1979). The metabolic clearance rate of ketone bodies has been found to increase in cold-acclimated fish (Jankowsky et al. 1984) indicating increased utilization. Perhaps as suggested by Jankowsky et al. (1984) enhanced ketogenesis with increased oxidation of ketone bodies may serve to spare carbohydrate. The low rates of pyruvate oxidation at low temperatures support this contention if one assumes the pyruvate oxidized in vivo is derived from carbohydrate. Voss (1985), however, reported higher pyruvate dehydrogenase activity in (*Onchorynchus mykiss*) acclimated to low temperature.

Alternatively, enhanced oxidation of ketone bodies relative to other substrates at low temperatures may serve to reduce the availability of acetoacetate for cholesterol synthesis. Cholesterol tends to stiffen membranes and reduced cholesterol content of membranes may serve to counteract the decreased fluidity caused by low temperature.

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Sea Growth and Time of Migration of Anadromous Arctic Char (*Salvelinus alpinus*) from the Vardnes River, in Northern Norway

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Berg, O. K., and M. Berg. 1989. Sea growth and time of migration of anadromous Arctic char (*Salvelinus alpinus*) from the Vardnes River, in northern Norway. Can. J. Fish. Aquat. Sci. 46: 955–960.

The annual seaward migration of Arctic char (*Salvelinus alpinus*) from the Vardnes River, northern Norway usually takes place early in summer, between the end of May and the beginning of June. A period of very fast growth was recorded immediately following the entry of char into the sea. Mean daily growth rates of both small and large char decreased with increasing length of time spent at sea, particularly after the end of June. Almost no further increase in length took place in the sea after the beginning of July. Sea temperature was low during this early growth period, rising to above 10°C during the period when sea char growth declined. Char appeared to be especially well adapted to low temperatures, since their growth rate during this early period was from two to four times faster than that recorded for sympatric sea trout (*Salmo trutta*). The results support the hypothesis that sea temperature may be one of the factors that control the southern distribution of anadromous Arctic char.

La migration annuelle de l'omble chevalier (*Salvelinus alpinus*) vers la mer à partir de la rivière Vardnes dans le nord de la Norvège se produit habituellement au début de l'été, de la fin de mai au début de juin. On a enregistré une période de croissance très rapide tout de suite après l'arrivée de l'omble en mer. Le taux de croissance journalier moyen tant chez les petits que chez les gros individus a baissé à mesure que la durée du séjour en mer augmentait, en particulier après la fin de juin. Il n'y a eu presque pas d'accroissement ultérieur en longueur après le début de juillet. La température de la mer a été basse pendant cette période de croissance précoce, s'élevant à un peu plus de 10°C au moment où la croissance de l'omble en mer diminuait. Les ombles semblaient particulièrement bien adaptés à de basses températures, puisque leur rythme de croissance au cours de cette période précoce a été de deux à quatre fois plus rapide que celui enregistré pour la truite brune (*Salmo trutta*) sympatrique. Les résultats étayent l'hypothèse voulant que la température de la mer soit l'un des facteurs qui limitent la répartition au sud de l'omble chevalier anadrome.

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The reasons underlying the seemingly intra- and interspecific synchronization in northern latitudes of the annual migration of fish from the rivers to the sea are still largely unknown (see e.g. Montgomery et al. 1983). Such migrations are often initiated by environmental stimuli (Ruggles 1980), which may, for example, facilitate the necessary osmotic adaptation to sea water and diminish the risks of predation.

Few salmonids that remain at sea for one year or more have been captured during their first summer in the sea. Their growth rates during the first few months at sea have therefore largely remained unknown. Berg and Berg (1987a) analysed the data from tagging experiments in the Vardnes River 1956–70, and showed that for the sea trout (*Salmo trutta*) in northern Norway, an especially favourable period of growth in the sea existed before the beginning of July. They suggested that the timing of the seaward migration was closely regulated to take full advantage of the more favourable feeding conditions that prevailed in the sea. Later in summer, growth rate declined resulting in similar growth in the sea and in freshwater. Timing of the upstream migration into the river was more variable than that of the downstream migration.

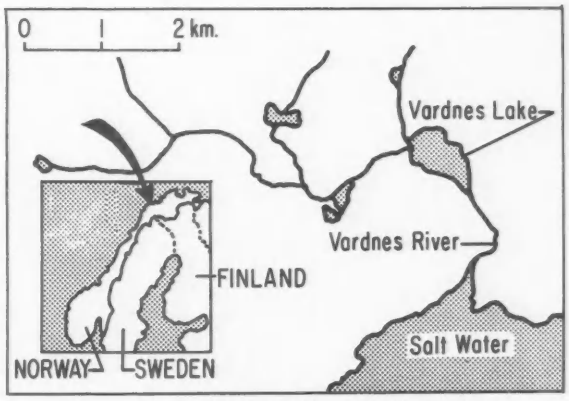

FIG. 1. Map showing the position of the Vardnes River.

The aim of the present study was to determine whether any differences in the growth patterns of Arctic char (*Salvelinus alpinus*) in the sea were related to differences in the respective times of descent and ascent in the Vardnes River during the

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summer. These growth patterns have been compared with previously published data for sea trout and with those for sea temperature.

Material and Methods

Traps to catch both descending and ascending anadromous salmonids were operated continuously during the period the fish were migrating down- or upstream in the Vardnes River (Fig. 1) over 12 yr during the periods 1956–63 and 1967–70. The traps (one for descending and one for ascending fish) captured all migrating fish under normal conditions, but not during floods.

The traps were situated in a small waterfall, close to the river mouth (Berg 1977). The anadromous char (Mathisen and Berg 1968; Jensen and Berg 1977) were individually tagged with a numbered Carlin tag attached to the base of the dorsal fin. Total length (to the nearest centimetre) and weight (to the nearest 10 g) were recorded for each fish each time it was captured. Individual daily growth rate was calculated from the total growth in length divided by the number of days between successive captures.

A total of 6165 sea char were tagged, either when descending or ascending. The total number of recaptures made in the traps was 3468, 1610 of which were of anadromous char captured first when descending and subsequently when ascending the river after their sojourn in the sea. The data for these recaptured fish were used to calculate the growth rates. Individual sea char were captured in the traps as many as nine times.

In addition, growth rate data were obtained for 69 first-time migrants and for 205 repeat migrants caught in the sea by various types of fishing gear. The quality of length and weight data from fishermen were inferior to those obtained in the traps. These captures have been used as a control of the validity of the trap data.

Growth data covering the periods of residence in the sea were grouped by 15-d intervals according to the respective times of descent and ascent, or of capture in the sea during the summer. The data for all study years and for all char longer than first-time migrants were pooled in the growth analyses. This could safely be done because no marked annual or monthly differences existed in the initial length of the different groups of char at the time of their descent to the sea.

Although tagging may retard the growth rate of salmonids (Power and Shooner 1966; Saunders and Allen 1967; Berg and Berg 1987b), no evidence of this was observed in the present study. Comparison between the mean lengths of ascending untagged and tagged fish revealed that the mean lengths were nearly identical for both groups of ascending first-time migrants (tagged fish $N = 859$, length = 27.3 (mean) ± 0.1 (SD) cm; untagged $N = 595$, length = 27.1 ± 0.1 cm) and second-time migrants (tagged fish $N = 528$, length = 34.0 ± 0.1 cm; untagged $N = 84$, length = 33.9 ± 0.1 cm). It was therefore concluded that the data could be used in an analytical study of the growth of sea char.

The sea temperature (Fig. 2), at 2–3 m below the surface, was recorded daily in the middle of the fjord outside the mouth of the Vardnes River.

Results

Growth in the sea

The mean duration of residence in the sea of all size groups of anadromous char from the Vardnes River was 48 d. Details of the periods of residence in the sea and in freshwater have been provided by Mathisen and Berg (1968), for the period 1958–62.

The data for the daily growth rates of first-time migrants during the sea sojourn are shown in Table 1 (except 1968 smolts, see below). The data indicate that mean daily growth is lower the later the descent to the sea is made, as well as with later ascent from the sea. A significant negative correlation ($r = -0.41$, $P < 0.001$) was found between the mean daily increase in length for the individual first-time migrants and the time of their ascent, indicating a gradual decrease in growth rate during the summer. This trend was in particular noticeable in the mean daily growth increment data of those fish which ascended later. The mean sea temperature (Fig. 2) increased from 7°C to about 10°C during this same period. Arctic char, when they have reached the smolt stage, thus seem able to grow well even at these low sea temperatures.

The decrease in growth between the first (mean 2.2 ± 1.3 mm·d^{-1}) and the second half (mean 1.3 ± 0.8 mm·d^{-1}) of July was the greatest recorded (Table 1, $P < 0.001$, t-test) among

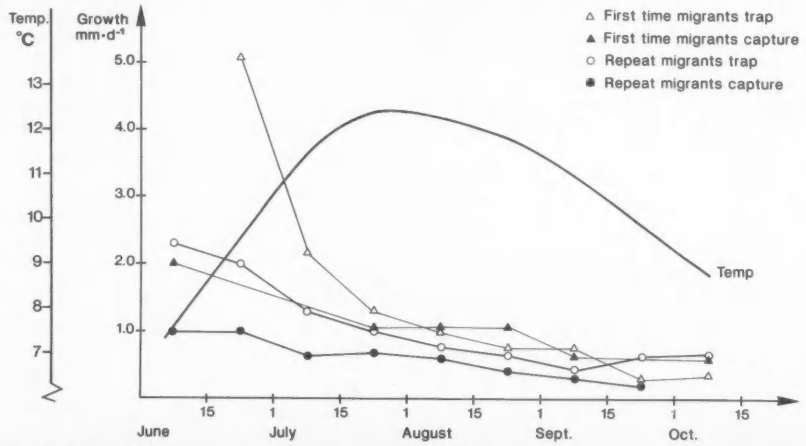

FIG. 2. Mean daily growth in length of char captured in the traps when ascending (trap), or captured in the sea (capture), plotted in relation to sea temperature.

TABLE 1. Mean daily growth in length (millimetres), of char that descended as smolts, between various times of capture upon descent and the initial time of their subsequent ascent of the Vardnes River. Data for 11 yr (1968 data excluded, see text).

Descent time		*N*	Mean size of smolts	Mean growth	Ascent time: 16–30 June	1–15 July	16–31 July	1–15 Aug.	16–31 Aug.	1–15 Sept.	16–30 Sept.	1–15 Oct.
					Mean daily growth increment (millimetres)							
May	1–15	9	24.3	1.9		2.4	0.8					
	16–31	76	23.6	2.0	3.2	2.5	1.2	0.7	0.1			
June	1–15	426	23.0	1.4	8.0	2.2	1.2	0.9	0.8	0.6	0.3	0.4
	16–30	119	22.5	1.5		1.9	1.6	1.4	0.8	3.1		0.3
July	1–15	1	20.3	0.7				0.7				
Mean					5.1	2.2	1.3	1.0	0.8	0.8	0.3	0.4
N					5	203	259	121	22	15	3	3

TABLE 2. Mean daily growth in length (millimetres), of char that descended as repeat migrants, between various times of capture upon descent and the initial time of their subsequent ascent of the Vardnes River.

Descent time		*N*	Mean size of migrants	Mean growth	Ascent time: 1–15 June	16–30 June	1–15 July	16–31 July	1–15 Aug.	16–31 Aug.	1–15 Sept.	16–30 Sept.	1–15 Oct.
					Mean daily growth increment (mm)								
April	16–30	5	35,4	1.5			1.4		1.9				
May	1–15	50	35,8	1.0	2.5	1.1	1.1	0.5	0.9		0.1		
	16–31	342	34,0	1.2		2.1	1.3	1.0	1.0	0.5	0.4	0.5	1.2
June	1–15	366	31,2	1.2	2.2	2.1	1.4	0.9	0.8	1.0	0.4	0.8	0.3
	16–30	16	29,8	1.7			1.8	1.9	0.4	0.8			
Mean					2.3	2.0	1.3	1.0	0.8	0.7	0.4	0.7	0.7
N					2	21	427	259	41	13	10	4	2

TABLE 3. Mean daily growth in length (millimetres), of decending repeat migrant char, between the time of their descent and of their capture in the sea.

Descent time		*N*	Mean	Capture: 1–15 June	16–30 June	1–15 July	16–31 July	1–15 Aug.	16–31 Aug.	1–15 Sept.	16–30 Sept.
				Mean daily growth increment (millimetres)							
April	16–30	1	0.6	0.6							
May	1–15	17	0.6	0.3	1.3	0.6	0.3		0.3		
	16–31	109	0.8	1.3	0.9	0.8	0.8	0.8	0.5	0.3	0.2
June	1–15	78	0.7		0.8	0.7	0.9	0.6	0.4	0.4	
Mean				1.0	1.0	0.7	0.8	0.6	0.4	0.3	0.2
N				6	25	91	46	22	11	2	2

ascending char. The mean sea temperature increased to above 11°C during this time (Fig. 2). Note that those fish that ascended late, were also those that had resided in the sea during the early period of high growth rates (last part of June and first part of July), and may have grown as fast in the sea during that period as those that migrated upriver early, in which case the decrease in growth in late July will have been even more marked than that suggested by the decrease in average growth found over the two periods.

The gradual decrease in the mean daily growth rate ($r = -0.25$, $P < 0.001$) among repeat migrant char (Table 2) ascending late was found again. This indicates that the factors influencing the growth of first-time migrants also apply to repeat migrants.

The growth data for char captured at sea show a similar pattern to those for the trap-caught char (Table 3), i.e. fish caught during the first and second halves of June (1.0 ± 0.7 mm·d^{-1})had higher ($P < 0.01$, *t*-test) growth rates than those caught later (0.7 ± 0.6 mm·d^{-1}). This supports the general validity of the trap data for the pattern of growth in the sea.

The overall length increment during the period of residence in the sea of both first time and repeat migrants which descended

TABLE 4. Mean increase in length (centimetres) of the different size groups of char during their residence in the sea. Downstream migrants grouped by (A) month of descent and (B) month of ascent.

A	Descending month April	May	June	July
First time migrants		9.7	6.1	3.7
Second time migrants	14.0	6.3	4.9	
Repeat migrants	11.0	5.1	5.4	

B	Ascending month June	July	Aug.	Sept.	Oct.
First time migrants	5.0	6.9	5.2	5.5	4.7
Second time migrants	6.3	5.5	4.9	5.0	
Repeat migrants	6.1	5.1	7.7	5.1	9.5

early was greater than that of those which descended later (Table 4). Also, those that ascended early (before the middle of July) showed a significantly ($P < 0.001$, t-test) greater total increase in length (6.3 ± 4.3 cm) than those that ascended late (5.3 ± 3.4 cm). A similar finding applied to those fish that had descended before the second half of June. This shows that almost no further increase in length took place in the sea after the beginning of July. Few char enter the Vardnes River after the beginning of August.

Timing of the Seaward Migration and Subsequent Growth

Arctic char generally migrate seawards earlier than sea trout (Fig. 3).

A regression analysis of the individual growth data for first-time migrants in all the investigated years revealed no significant correlation ($P \sim 0.31$, $r \sim -0.04$) between the time of onset of the seaward migration and the subsequent daily increase in length. However, a significant negative correlation ($P < 0.001$, $r = -0.15$) was noted when the data for 1968 were excluded from the calculations. The timing of the seaward migration of the repeat migrant char was normal in 1968, compared with previous years, but the smolts migrated extremely late that year, 50% of the cumulative descent of the smolts occurring about 2 wk later than usual. The data for this year have therefore been excluded from the calculations of the daily growth in length of the first-time migrants (Table 1).

There was no significant relation ($P \sim 0.27$, $r \sim 0.04$) between daily mean growth and time of onset of descent of the repeat migrants (Table 2).

Discussion

There were marked dissimilarities in the patterns of summer growth in the sea of the populations of sea char and sea trout which, during their freshwater phases, co-habited the Vardnes

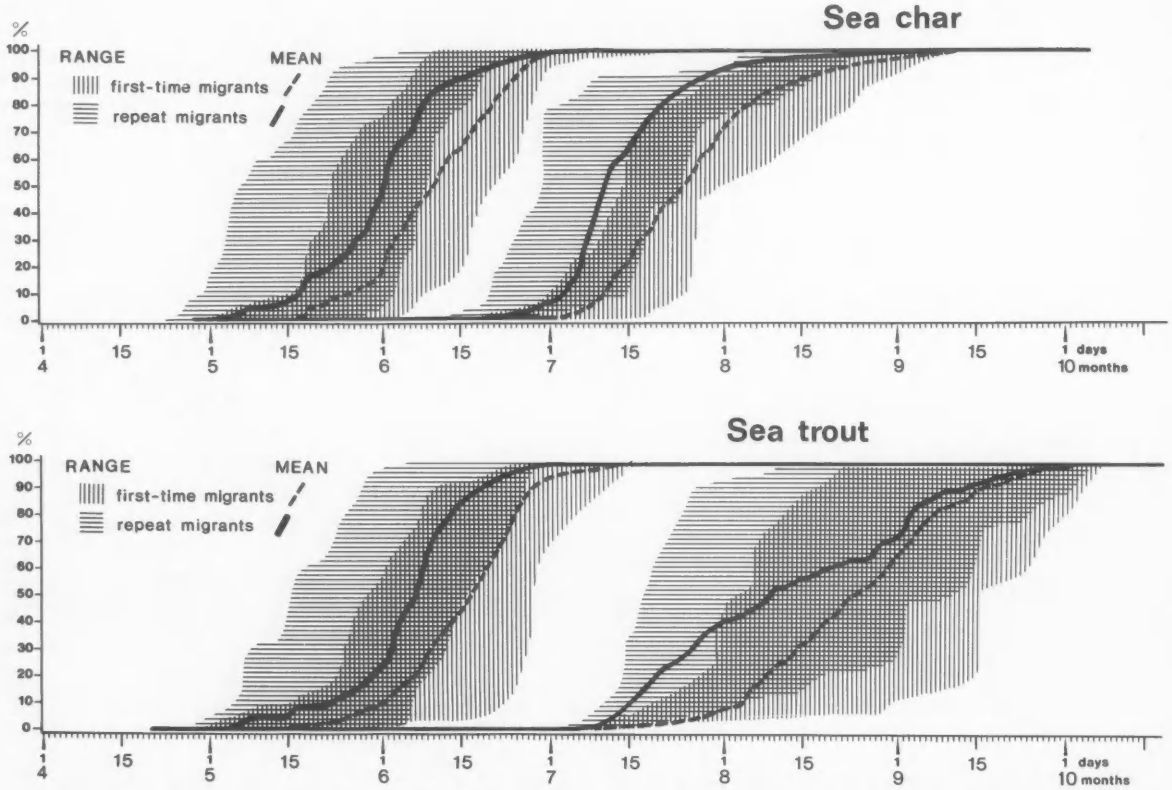

FIG. 3. Cumulative captures of sea char (upper half) and sea trout (lower half) as descending (left-hand) or ascending (right-hand). The most extreme periods of the downstream and of the upstream migrations are hatched. Data for first-time migrants (hatched) are separated from those of repeat migrants (solid line).

River. The period of maximum growth of the sea trout from the Vardnes River took place at the end of June or at the beginning of July (Berg and Berg 1987a), and the mean growth rate of sea trout was still high in the sea (about 1.5 $mm \cdot d^{-1}$) when char growth had apparently ceased. Evidently the growth rate of sea trout declined later in the summer and less abruptly than that of char.

The absence of further growth of the late-ascending sea char is probably not due to a dearth of food in the sea: the feeding niches in the sea of the char and the trout seem to be similar (Grønvik and Klemetsen 1987) and similar proportions of sea trout (0.68, $N_{tot} = 2093$) and of char (0.62, $N_{tot} = 534$) from the Vardnes River have been reported from catches in gill nets near the shore. This accords with the previous findings of Moore (1975) and Sekerak et al. (1976).

Next to food supply, water temperature is the parameter that most affects the growth rate of poikilotherms. Sea temperature increases throughout most of the period of char ascent in the study region. The daily growth rate of sea char early in the summer is two to four times higher than that of sea trout (Berg and Berg 1987a). Our results thus suggest that Arctic char grow better than trout at low water temperatures in the sea. In the Sylvia Grinnel River, Baffin Island, Canada, char that ascend late (between July 24 and September 5) show considerable growth (Grainger 1953) but the sea temperature in that region rarely exceeds 3°C (Moore 1975). Dempson and Kristofferson (1987) found that the anadromous char populations along the Labrador coast, Canada, had an early onset of downstream migration. The average sea temperature in that region during the second half of July is 7.6°C, about 5°C lower than that recorded in the fjord off the mouth of the Vardnes River. Arctic char thus possess an outstanding ability to grow well at low sea temperatures.

Because char can grow well in cold seawater, their residence at sea may be longer where sea is cold than in warmer areas. The average minimum duration of sojourn at sea before capture of Arctic char from Nain Bay, Labrador, was 57.1 d ($N = 139$), while those from Tikkoatokak Bay, Labrador, remained at sea for an average of 52.3 d ($N = 269$) (Dempson and Kristofferson 1987). These values are considerably higher than the 48 d recorded for char from the Vardnes River.

The timing of the migration of salmonids to sea should be related to the onset of favourable conditions for growth. One would expect that the timing of the spring migration seawards would be both precise and simultaneous within a species, so as to gain maximum benefit from the favourable growth conditions in the sea. Because the growth of char in the sea decreases the later the time of descent, in contrast to sea trout which grow better later, one would expect to find that the downstream migration of the char would take place earlier than that of the sea trout. This expectation was supported by the trap records for the periods of descent of these two species (Fig. 3). The timing of the downstream migration of sea char in other areas apparently also occurs early in the summer (see e.g. Grainger 1953; Johnson and Campbell 1975; Moore 1975; Johnson 1980; Dempson and Kristofferson 1987).

Once past the most favourable period for growth in the sea, the difference between the growth rates of char in the sea and freshwater diminishes, thus allowing a greater latitude in subsequent behavioural strategy. A greater variation in the period of ascent might therefore be expected compared with the period of descent, and is visible (Fig. 3) as the periods of ascent of both char and trout being more extended in time. A considerable variation in the period of ascent of sea char into the Fraser River, Labrador, was also recorded by Dempson and Green (1985). Both the sea char and the trout in the Vardnes River spawn at the beginning of October.

The distribution of Arctic char may be limited by the prevailing sea temperature in summer. In Norway, anadromous char are generally distributed north of 65°N (e.g. Jensen 1981), while the distribution extends south to 49°N on the east coast of North America (Johnson 1980). Jensen and Steine (1980) and Jensen (1981) have proposed that an average sea surface temperature of 14.0°C limits the southern distribution of anadromous char in Norway. Gjedrem (1975) found that char smolts, kept in cages after their transfer to the sea early in June 1974 at Averøy, about 300 km south of their customary southern distributional limit, behaved quite normally at first, but that the death rate increased dramatically from mid-August onwards. The sea temperature recorded at Hustadvika, in the same area, reached its highest value (about 14.5°C) in the latter part of August in 1974 (data supplied by Norwegian Oceanographic Data Center). The present results support the hypothesis that sea temperature may be one of the main factors that determines the southern distributional limit of anadromous char.

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A System of Simultaneous Dynamic Production and Forecast Models for Multispecies or Multiarea Applications

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A system of simultaneous dynamic production models is presented for multispecies or multiarea applications. The system of equations arises by using a linear dynamic production model with one equation for each area or species. The parameter estimation for the system of equations is particularly efficient when some of the parameters are assumed to have the same value in more than one equation.

Un système de modèles de production dynamique simultanés est présenté en vue de son application à plusieurs espèces ou dans plusieurs zones. Le système d'équations provient d'un modèle linéaire de production dynamique à une équation pour chacune des zones ou des espèces. L'estimation des paramètres pour le système d'équations est particulièrement efficace lorsque l'on suppose que certains paramètres ont la même valeur dans plus d'une équation.

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Surplus production models are useful and widely employed tools to identify target levels of yield and effort from a time series of catch and effort data (Gulland 1983). Parameter estimation for production models is essentially a curve fitting process, and the most reliable estimates are obtained when there is a wide range of effort levels covering both the ascending and descending portions of the catch and effort curve. Thus, if the time series of catch and effort data is short and the effort range is restricted, the application of a production model may not be advisable. In these instances, composite production modeling has occasionally been used if catch and effort data from different geographic sites are available. This approach uses, from different regions, catch and effort adjusted by a measure of the habitat area. The resulting catch and effort per unit of habitat from the different regions are plotted on the same graph to identify the optimum catch and effort expressed per unit of habitat (Munro 1979; Caddy and Garcia 1982). Munro (1979) plotted annual reef fish catches per square kilometre of reef against the number of canoes per square area of reef from different parishes in Jamaica and observed a dome-shaped "production" curve. Combining regional catch and effort into a single production curve is sensitive to the estimate of the habitat, assumes equilibrium catch and effort at each region, and assumes an absence of regional production differences and interactions in stock levels between regions.

When catch and effort data are available on either a regional basis, such as for islands in an archipelago, or for a number of similar species in a multispecies fishery, the data are frequently aggregated and fit to a single production model. However, an alternative approach, which I develop in this paper, is to simultaneously fit a system of production models to the data by using one equation per area or species. When some of the parameters (e.g. the intrinsic rate of increase or catchability) can be assumed the same for each area or species, then the number of parameters to be estimated by the system will be reduced, and the estimation power increased. Further, when some areas or species are heavily fished and others are lightly fished, the simultaneous system of equations is fit to the full effort range rather than just the ascending or descending portion of the production curve.

A major issue in parameter estimation with production models is whether to (1) assume catch levels are in equilibrium as a function of effort and use the simple, usually linear, estimators or (2) not assume that catch levels are equilibrium levels and use more complex, often nonlinear, dynamic estimators. In situations where fishing effort displays substantial annual variation, such as in a new, rapidly developing fishery, catch levels most likely do not represent equilibrium levels. Simulation studies have shown that, when catch is not in equilibrium with effort, parameter estimates based on the assumption of equilibrium conditions can have larger variances and biases than the parameter estimates obtained from dynamic estimators (Mohn 1980). Dynamic estimators have been derived for both the Schaefer and the Pella and Tomlinson production models (Pella and Tomlinson 1969; Schnute 1977). Both dynamic estimators require nonlinear estimation methods, but for the Schaefer model, the dynamic estimator has a good linear approximation, which will be used as the basis for the proposed system of equations (Schnute 1977).

System of Production Equations

To describe the linear approximation to the dynamic Schaefer model, let C_n and E_n be the annual catch and effort in year n, and let the catch per unit effort for year n (C_n/E_n) be denoted as U_n. Then the intrinsic rate of population increase (r), the

catchability (q), and the unexploited biomass (k) can be estimated from the following regression (Schnute 1977):

(1) $\ln(U_n/U_{n-1}) = r - q(E_{n-1} + E_n)/2 - (r/qk)(U_{n-1} + U_n)/2.$

With the estimates of r, q, and k, the catch in year $n + 1$ can be predicted as a function of the effort in year $n + 1$ as follows (Schnute 1977):

$$(2)\quad C_{n+1} = ((qk/r)E_{n+1}) \ln\left[1 + \frac{(r - qE_n)}{(r - qE_{n+1})} \times \left(\frac{\exp(r - qE_{n+1}) - 1}{1 - \exp(-(r - qE_n))}\right)\left(1 - \exp\left(\frac{-rC_n}{qkE_n}\right)\right)\right]$$

While under equilibrium conditions, the traditional Schaefer model is

(3) $C = qkE(1 - (q/r)E).$

When the notation in equation (1) is simplified, the equation is a linear regression with two independent parameters and can be written as

$$Y_n = A + BX_n + CZ_n + \text{error};$$

where

$$Y_n = \ln(U_n/U_{n-1}),\ X_n = (E_{n-1} + E_n)/2, \text{ and}$$

$$Z = (U_{n-1} + U_n)/2.$$

When catch ($C_{i,n}$) and effort ($E_{i,n}$) data are available for the ith geographic region (stock) or the ith species ($i = 1,\ldots,I$), then a system of simultaneous equations can be written as

$$\begin{aligned} Y_{1,n} &= A_1 + B_1X_{1,n} + C_1Z_{1,n} + \text{error}_1 \\ &\vdots \\ Y_{I,n} &= A_I + B_IX_{I,n} + C_IZ_{I,n} + \text{error}_I\ ; \end{aligned}$$

where the parameters A_i, B_i, and C_i are r_i, $-q_i$, and $-r_i/(q_ik_i)$, respectively, for the ith region or ith species. Likewise, the variables $Y_{i,n} = \ln(U_{i,n}/U_{i,n-1})$, $X_{i,n} = (E_{i,n-1} + E_{i,n})/2$, and $Z_{i,n} = (U_{i,n-1} + U_{i,n})/2$. The parameters can be estimated by ordinary least squares methods; however, econometric theory shows that, if the errors (error_i) are correlated, then generalized least squares regression (or what is sometimes referred to as Zellner regression, which uses the covariance between the error variables) is more efficient (Pindyck and Rubinfeld 1981). An important advantage in using a system of production models comes when some of the parameters to be estimated are assumed to have the same value between the equations. For example, by assuming that r_i is the same for all i, the number of parameters to be estimated is reduced from $3I$ to $2I + 1$.

The use of simultaneous equations is not restricted to just the dynamic Schaefer production model estimator. Other dynamic production models, such as that of Pella and Tomlinson (1969), as well as the more widely used equilibrium production model estimators can be used as the bases for the system of equations. Autoregressive models that regress Y_n on Y_{n-1} and effort or models that incorporate regional environmental variation can also be formulated as a system of equations.

Both SHAZAM (White and Horsman 1985) and SAS (1984) econometrics computer packages have routines to estimate regression coefficients described by a system of linear equations. The subsequent application of the system of equations to lobster catch and effort data used the SHAZAM program on an IBM-AT.

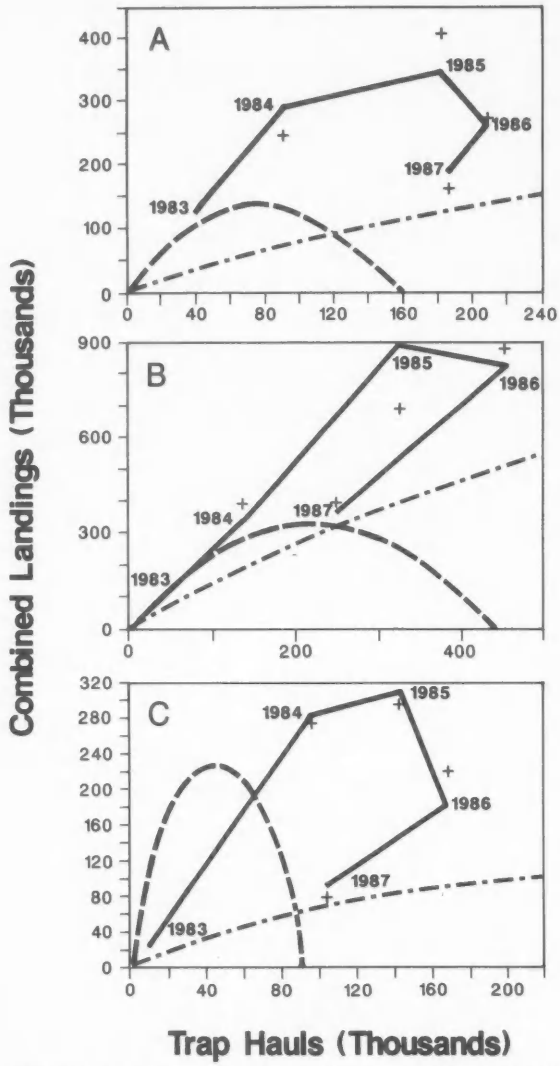

FIG. 1. The actual (——), predicted (+ + +), 1988 forecasted (— · — · —), and equilibrium (- - -) combined landings for spiny and slipper lobsters by trap hauls at (A) Necker Island, (B) Maro Reef, and (C) Gardner Pinnacles.

Application to the Hawaii Lobster Fishery

Catch and effort data are available for 1983–87 for a commercial lobster fishery for three banks (Necker Island, Gardner Pinnacles, and Maro Reef) in the Northwestern Hawaiian Islands. The fishery traps primarily the spiny lobster *Panulirus marginatus* and the slipper lobster *Scyllarides squammosus*. Catch is reported by bank and species, whereas effort is reported only by bank because both species can be caught together in the same trap. In the subsequent analysis, the combined catch and total effort for slipper and spiny lobsters are used.

Over the period 1983–87, large variations in effort occurred on all three banks; hence, the dynamic production model was required because catch levels were not in equilibrium with effort (Fig. 1). When the catch and effort data from the three banks were fit separately to the dynamic production model, each had 4 yr of data with three parameters to be estimated. None of the fits to the dynamic production models produced parameter estimates that were statistically significant (t-test, $P = 0.05$). When a system of three simultaneous equations were used, there were 12 yr of data with nine parameters to be estimated. The resulting parameter estimates were within expected levels for two of the three banks, but for one of the banks, negative estimates of r and k were obtained. When the parameter r was restricted to be the same for all three banks, the number of parameters were reduced to seven, the fits appeared good at all banks, and all parameter estimates were statistically significant ($P<0.05$) (Fig. 1). Given the short time series, there was no difference when the simultaneous regression used ordinary least squares regression or Zellner regression, which uses the autocorrelation in the errors.

Estimates of r, q, and k were used to forecast the 1988 yield curve (equation 2) and the equilibrium surplus production curve (equation 3) for each bank (Fig. 1). The substantial differences between the nonequilibrium catches and the predicted equilibrium production curves highlight the difference between production levels obtained in the early stages of a developing fishery and those that can be expected after equilibrium has been achieved. Bootstrapping estimated the standard errors for the bank maximum sustainable yield (MSY) averaged 50% of the bank MSY levels and, for bank fishing effort that achieves MSY, the standard errors averaged 31% of the effort levels. The standard errors should decline as the length of the time series of catch and effort data increases.

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Concentration of Infectious Hematopoietic Necrosis Virus from Water Samples by Tangential Flow Filtration and Polyethylene Glycol Precipitation

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Batts, W. N., and J. R. Winton. 1989. Concentration of infectious hematopoietic necrosis virus from water samples by tangential flow filtration and polyethylene glycol precipitation. Can. J. Fish. Aquat. Sci. 46: 964–968.

Infectious hematopoietic necrosis virus (IHNV) was concentrated from water samples by polyethylene glycol (PEG) precipitation, tangential flow filtration (TFF), and by a combination of TFF followed by PEG precipitation of the retentate. Used alone, PEG increased virus titers more than 200-fold, and the efficiency of recovery was as great as 100%. Used alone, TFF concentrated IHNV more than 20-fold, and average recovery was 70%. When the two techniques were combined, 10-L water samples were reduced to about 300 mL by TFF and the virus was precipitated with PEG into a 1 to 2 g pellet; total recovery was as great as 100%. The combined techniques were used to isolate IHNV from water samples taken from a river containing adult sockeye salmon (*Oncorhynchus nerka*) and from a hatchery pond containing adult spring chinook salmon (*O. tshawytscha*). The combination of these methods was effective in concentrating and detecting IHNV from water containing only three infectious particles per 10-L sample.

On a concentré le virus de la nécrose hématopoiétique infectieuse (VNHI) présent dans des échantillons d'eau par la technique de précipitation au polyéthylèneglycol (P.E.G.), la filtration par écoulement tangentiel, et par une combinaison de ces deux méthodes, la filtration étant suivie de la précipitation au P.E.G. du rétentat. Par le P.E.G. seul, on a obtenu une augmentation du titre de plus de deux cent fois, la récupération atteignant 100 %, et par la filtration seule, une augmentation du titre de plus de 20 fois, pour une récupération moyenne de 70 %. Lorsque l'on a combiné les deux techniques, il a été possible de réduire des échantillons d'eau de 10 L à 300 mL environ au moyen de la filtration par écoulement tangentiel et de précipiter, avec le P.E.G., le virus qui a été incorporé à des pastilles de 1 à 2 g. La récupération a atteint 100 %. Une combinaison de ces techniques a permis d'isoler le VNHI présent dans des échantillons d'eau prélevés dans une rivière fréquentée par le saumon nerka adulte (*Oncorhynchus nerka*), ainsi que dans une écloserie abritant des saumons quinnats adultes (*O. tshawytscha*). En combinant ces méthodes, on a réussi à concentrer et à déceler le VNHI dans de l'eau contenant seulement trois particules infectieuses par échantillon de 10 L.

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Infectious hematopoietic necrosis (IHN) causes the loss of millions of salmon and trout each year. The causative agent, infectious hematopoietic necrosis virus (IHNV), has been isolated from salmonid fish at many locations in western North America, where it is enzootic (Pilcher and Fryer 1980). The virus has spread to other parts of the United States, Japan, Taiwan, France, and Italy through the shipment of infected fish and eggs. Although IHNV may be transmitted in the water by passing from an infected fish to a susceptible host, the virus is difficult to recover from water samples by direct inoculation of cell cultures unless present at a relatively high concentration (Leong and Turner 1979; Mulcahy et al. 1983a). To learn more about the epizootiology of IHNV and to develop an efficient means of quantifying the low levels of virus that may be present in natural waters and fish culture facilities, we compared several methods of concentrating IHNV from large volumes of water.

Highly stable viruses such as enteroviruses have been adsorbed onto filter membranes and removed by eluants as an efficient method for concentrating these viruses from water and sediment samples (Rao and Labzoffsky 1969; Hill et al. 1972; Sobsey and Jones 1979). Attempts in our laboratory to recover IHNV by membrane adsorption were unsuccessful due to the sensitivity of this virus to pH shifts and the lack of an efficient eluant (data not shown).

Two-phase systems have been used effectively for the separation and concentration of viruses (Albertsson 1967). Infectious pancreatic necrosis (IPN) virus, a birnavirus of fish, has been concentrated more than 100-fold with a 50–70% recovery by a two-phase system composed of polyethylene glycol (PEG) and dextran sulfate (Grinnell and Leong 1979); and a 10-fold concentration of IPN virus from tissue culture fluid using 10% PEG was reported by Cohen et al. (1973).

The animal rhabdoviruses, vesicular stomatitis virus and rabies virus, have been concentrated and purified from cell culture fluids by PEG precipitation followed by ultracentrifugation (Wunner 1985); and precipitation by PEG was used to concen-

trate the salmonid rhabdoviruses of viral hemorrhagic septicemia and IHN from cell culture fluids (de Kinkelin 1972). In the present study, we concentrated IHNV from 200-mL water samples by the addition of PEG, followed by low speed centrifugation. This procedure resulted in an increased virus titer in the pellet of greater than 200-fold.

Tangential flow filtration (TFF) allows particles of low molecular weight to pass through a large-area membrane filter but retains viruses and macromolecules. This technique was used to concentrate IHN and IPN viruses from 10 and 50-L water samples by Watanabe et al. (1988). After TFF, the retained volume of about 250 mL was titered directly or concentrated further by ultracentrifugation, resulting in the detection of low levels of IHN and IPN virus from water samples with high efficiencies of recovery.

To develop a simple and efficient method for detecting very low levels of IHN virus in hatchery and natural water supplies, we compared TFF, PEG precipitation, and a combination of the two techniques. Using these methods, we were able to detect IHNV in water samples from the Cedar River, Washington, known to be holding sockeye salmon (*Oncorhynchus nerka*) infected with the virus, and from ponds at the Leavenworth National Fish Hatchery containing adult chinook salmon (*O. tshawytscha*). The laboratory and field tests indicated that the detection limit for the combined techniques was about three plaque-forming units (PFU) in a 10-L water sample.

Materials and Methods

Plaque Assay

Epithelioma papulosum cyprini (EPC) cells (Fijan et al. 1983) were suspended in minimum essential medium (MEM; Gibco) containing 5% fetal bovine serum (FBS; Gibco), 2 mM L-glutamine (Gibco), 0.3% tryptose phosphate (Difco), and 12 mM tris(hydroxymethyl)aminomethane (MEM-tris; Sigma). The cells were seeded into eight-well multiplates (Miles Scientific) at a density of 2×10^6 cells·well^{-1} and incubated at 25°C overnight. To avoid plasmolysis, we diluted water samples for direct plating with an equal volume of MEM-tris. Resuspended PEG pellets were diluted with MEM-tris supplemented with amphotericin B at 2.5 μg·mL^{-1}, penicillin at 100 IU·mL^{-1}, streptomycin at 100 μg·mL^{-1} (Gibco), and gentamycin sulfate at 100 μg·mL^{-1} (U.S. Biochem. Corp.). We inoculated 0.1 mL of sample and serial $\log_{10}$ dilutions to replicate, drained monolayers, and allowed the virus to be adsorbed for 30 min at 20°C before we added 2 mL methyl cellulose (0.75%) overlay to each well (Mulcahy et al. 1982). The plates were incubated for 7 or 8 d at 15°C to allow plaque formation before fixation and staining.

Virus Stocks

We used two isolates of IHNV in this study. For comparison and testing of the concentration methods, we used a strain of IHNV isolated from Cedar River sockeye salmon fry. This isolate was also used as a positive control during recovery of IHNV from Cedar River water samples. Virus was passed three times through EPC cells and aliquots frozen at −70°C. The positive control for detection of IHNV in water samples at the Leavenworth National Fish Hatchery was an isolate obtained the previous year from spawning adult chinook salmon. This isolate was passed once on EPC cells, then frozen at −70°C. Virus isolates were thawed and diluted to appropriate levels for experiments.

Concentration Techniques

For PEG precipitation studies, known concentrations of IHNV from 10^{-2} to 10^3 PFU·mL^{-1} were prepared in UV-treated, filtered lake water. In these initial studies, virus particles were stabilized by adding FBS, 1 M tris, powdered MEM, and tryptose phosphate to make the samples equivalent to 1X MEM containing 6% serum. We removed a small portion of the stabilized mixture before adding PEG, to determine the initial concentration of IHNV in the 200-mL samples. We added PEG with an average molecular weight of 6000 (PEG-6000, EM Science) or 20 000 (PEG-20 000, Fisher Scientific) to give a 7% (w:w) solution, which was stirred overnight at 7°C. The samples were centrifuged ($6540 \times g$ for 90 min at 4°C) and the supernatants decanted. The PEG pellets were resuspended in 500 μL tris-buffered saline, and tested for IHN virus by plaque assay.

The Pellicon Cassette tangential flow filtration system was fitted with a membrane filter (Millipore) having 4650 cm^2 of filter area with a 100 000 molecular weight exclusion size. We prepared the filter for use by flushing through it 15 L of deionized water followed by 1 L of phosphate buffered saline (PBS). We used the filter operation procedures of Watanabe et al. (1988). Deionized water (10.2 L) was seeded with IHNV (Cedar River isolate), stabilized by the addition of FBS (0.1%), and a 200-mL sample was removed for determination of the initial virus titer. The filtration apparatus was operated for 10 min before we collected a 200-mL sample of filtrate solution for virus assay. Filtration was continued until the retained volume was reduced to about 100 mL. We performed two 100-mL backflushes with PBS to remove any virus retained on the filter membrane and tubing. These backflushes were combined with the retained volume to form the retentate solution. All samples were held on ice during the filtration runs. The initial sample, filtrate, and retentate were titered by plaque assay and the volumes of each were recorded. The filtration time required for 10 L was about 1 h.

To test the sensitivity of TFF combined with PEG precipitation, we processed 10.2-L volumes of deionized water seeded with one of three concentrations of IHNV. Each sample was supplemented with FBS (0.1%) and kept on ice during the TFF procedure. After TFF, we further concentrated each retentate (about 200–300 mL) by the addition of 7% (w:w) PEG-20 000, overnight mixing, and low-speed centrifugation as described. The IHNV titers of the samples and pellets were determined by plaque assay.

Field Tests

We used PEG precipitation alone to recover IHN virus from water samples of the Cedar River, Washington at each of nine dates during 1986. The samples were collected from a side-channel of the river containing several hundred spawning sockeye salmon. Virus particles were stabilized by adding FBS, 1 M tris, powdered MEM, and tryptose phosphate to make the mixture equivalent to 1X MEM containing 6% serum. The stabilized samples were transported to the laboratory on ice where they were clarified by centrifugation ($6540 \times g$, 10 min, 4°C) to remove bacterial and organic debris. The virus particles were precipitated by PEG-6000 as described, and the IHNV titer of the pellet was determined by plaque assay. On the same dates,

TABLE 1. Comparison of two molecular weights of polyethylene glycol (PEG) for concentration of selected levels of infectious hematopoietic necrosis virus. PEG was added at 7% w:w to 200-mL water samples seeded with virus. Calculated values based on dilution of virus solutions with measured titers are given in parentheses. BD = below detection limit for plaque assay.

Initial	Pellet			
PFU·mL^{-1}	Weight (g)	PFU·g^{-1}	Concentration factor (×)	Percent recovered
PEG-6000				
1.7×10^3	0.37	6.8×10^5	400	74
1.9×10^2	0.29	5.6×10^4	295	43
1.1×10^1	0.34	3.5×10^3	318	54
(1.7×10^0)	0.22	4.2×10^2	(247)	(27)
(1.7×10^{-1})	0.29	1.4×10^1	(82)	(12)
(1.7×10^{-2})	0.24	BD	—	—
PEG-20 000				
1.1×10^3	0.92	1.9×10^5	173	79
1.3×10^2	0.92	1.9×10^4	146	67
8.2×10^0	0.91	3.0×10^3	378	166[a]
(1.1×10^0)	0.88	2.3×10^2	(209)	(92)
(5.5×10^{-1})	1.09	1.0×10^2	(182)	(99)
(1.1×10^{-1})	0.82	BD	—	—
(5.5×10^{-2})	0.36	1.2×10^1	(218)	(39)
(1.1×10^{-2})	0.34	BD	—	—

[a]Recoveries in excess of 100% are probably due to the enhanced IHNV titer obtained with fish cells following contact with PEG (W. N. Batts and J. R. Winton, unpubl. data).

we collected 5–15 adult female salmon and tested the ovarian fluids for virus by plaque assay.

To quantify the amount of IHN virus shed by adult sockeye salmon, we collected 10.2-L water samples about 50 m above and below a large diameter pipeline crossing on the Cedar River that serves as an effective weir to block fish migration below the Landsburg Dam. Sockeye salmon were seen below, but not above, this obstacle. Virus particles in the water samples were stabilized by adding FBS (0.1%) and the samples were transported on ice to the laboratory. We filtered the samples by TFF, and further concentrated the virus particles in initial, filtrate, and retentate pools by PEG-20 000 precipitation. The IHN virus in each PEG pellet was titered by plaque assay.

We determined the level of IHNV in a spring chinook salmon adult holding pond at the Leavenworth National Fish Hatchery. After fish were crowded for 3 h during spawning procedures, we stabilized a 10.2-L sample of holding pond water by adding FBS (0.1%). The sample was stored overnight at 7°C and then filtered by TFF. Virus particles in the initial solution, filtrate, and retentate were precipitated by PEG-20 000, and the titers determined by plaque assay. As a positive control, an isolate of IHNV from Leavenworth spring chinook salmon was diluted to 2 PFU·mL^{-1} in 10.2 L of deionized water and processed identically.

Results and Discussion

Laboratory Tests of Concentration Techniques

Using direct inoculation of water samples onto cell cultures, it is difficult to detect fish viruses present at titers below about 1 PFU·mL^{-1}. For detection of virus below this level, a concentration method is required. When IHN virus was concentrated from water samples by PEG precipitation, the larger molecular weight PEG-20 000 generally provided a better efficiency of recovery than PEG-6000 (Table 1). Both types of PEG produced a concentration factor of about 200-fold at the virus levels tested, suggesting that the lower limit of IHNV detection was about 1 PFU·200 mL^{-1} for our precipitation and assay methods. Polson (1977) described the PEG precipitation procedure as a dehydration process, where long-chained PEG molecules trap water in their folds more efficiently than shorter-chained PEG molecules.

Water samples containing IHN virus at concentrations below the detection limit of the plaque assay yielded detectable virus after TFF, and we obtained excellent recovery and concentration when TFF was combined with PEG precipitation (Table 2). The virus titers of the filtrate solutions were always below detection limits indicating little, if any, IHNV was able to pass through the filter. The overall virus recovery after TFF and PEG precipitation ranged from 56 to 113% (recoveries in excess of 100% are probably due to the enhanced IHNV titer obtained with fish cells following contact with PEG, W. N. Batts and J. R. Winton, unpubl. data) and the virus was concentrated from 3375 to 4375-fold. The combination of TFF with PEG precipitation detected virus at less than 1 PFU·3 L^{-1} of sample.

TABLE 2. Concentration of three levels of infectious hematopoietic necrosis virus by a combination of tangential flow filtration followed by polyethylene glycol precipitation. The virus titer is expressed as PFU·mL^{-1} (PFU·g^{-1} for PEG pellets). Initial titers were calculated from dilution of measured virus solutions. The PEG pellet volume is the weight of the pellet from the retentate solution. BD = below detection limits of plaque assay.

Filtration run and samples tested	Volume (mL)	Virus titer	Total PFU	Concentration factor (×)	Percent recovered
1 Initial	10 000	1.2×10^0	1.2×10^4	1	(100)
Retentate	368	2.5×10^1	9.2×10^3	21	77
PEG pellet	(2.72 g)	4.9×10^3	1.3×10^4	4083	111[a]
2 Initial	10 000	1.6×10^{-1}	1.6×10^3	1	(100)
Retentate	318	3.3×10^0	1.0×10^3	21	63
PEG pellet	(1.66 g)	5.4×10^2	9.0×10^2	3375	56
3 Initial	10 000	1.6×10^{-2}	1.6×10^2	1	(100)
Retentate	320	BD	BD	—	—
PEG pellet	(2.51 g)	7.0×10^1	1.8×10^2	4375	113[a]

[a]Recoveries in excess of 100% are probably due to the enhanced IHNV titer obtained with fish cells following contact with PEG (W. N. Batts and J. R. Winton, unpubl. data).

TABLE 3. Detection of infectious hematopoietic necrosis virus from Cedar River wat samples (initial volume = 800 mL) by polyethylene glycol (PEG-6000; 7% w:w) precipitation. ND = not done; BD = below detection limit of plaque assay (less than one plaque in 24 wells).

Date (1986)	River flow ($m^3 \cdot s^{-1}$)	Positive fish (%)	Before precipitation PFU·mL^{-1}	After precipitation		Concentration factor (×)
				Weight (g)	PFU·g^{-1}	
08 Sep.	3.6	ND	BD	2.82	BD	—
15 Sep.	4.8	0	BD	2.48	BD	—
22 Sep.	5.8	0	BD	2.43	BD	—
29 Sep.	6.8	93	7.2×10^{-1}	1.73	4.8×10^{1}	67
06 Oct.	8.9	87	BD	2.00	BD	—
14 Oct.	10.5	100	7.2×10^{-1}	1.48	1.3×10^{1}	18
20 Oct.	10.6	100	7.2×10^{-1}	1.46	2.2×10^{1}	31
03 Nov.	11.2	60	BD	1.32	2.2×10^{0}	—
17 Nov.	12.1	100	1.4×10^{0}	2.45	BD	—

TABLE 4. Detection of infectious hematopoietic necrosis virus from a spring chinook salmon adult holding pond at the Leavenworth National Fish Hatchery by tangential flow filtration followed by polyethylene glycol (PEG-20 000; 7.0% w:w) precipitation. PEG pellet volume is the weight of the pellets from the retentate solutions and the mean PFU·g^{-1} of pellet is recorded instead of PFU·mL^{-1}.

Filtration run and samples tested		Volume	Virus titer	Total PFU	Concentration factor (×)	Percent recovered
Hatchery water:	Initial	10 000 mL	7.1×10^{0}	7.1×10^{4}	1	(100)
	Retentate	269 mL	1.1×10^{2}	3.0×10^{4}	15	42
	PEG pellet	1.51 g	1.5×10^{4}	2.3×10^{4}	2113	32
Positive control:	Initial	10 000 mL	1.8×10^{0}	1.8×10^{4}	1	(100)
	Retentate	292 mL	8.7×10^{1}	2.5×10^{4}	48	139
	PEG pellet	2.21 g	5.1×10^{3}	1.1×10^{4}	2833	61

The efficiency of TFF obtained in this study was similar to the results reported by Watanabe et al. (1988). These workers used TFF followed by ultracentrifugation to concentrate IHNV from water samples of the Metolius River in Oregon containing virus at an estimated 1 PFU·3 L^{-1}.

Field Tests of Concentration Techniques

We isolated IHNV from Cedar River water samples collected on five of the nine sampling dates (Table 3). The addition of PEG-6000 increased the virus titer on four of these dates. No virus was detectable in the supernatant after centrifugation showing that the precipitation technique was relatively efficient. The first date of virus isolation from water samples corresponded with the first date of detection of IHNV in samples collected from sockeye salmon spawning in the river. The prevalence of IHNV-positive fish rose from 0 to more than 90% in 1 wk. Mulcahy et al. (1983a) did not use a concentration procedure to detect IHNV levels up to 1600 PFU·mL^{-1} in 1979 and 32.5 PFU·mL^{-1} in 1980 in water samples collected from a side-channel of the Cedar River. Sockeye salmon spawning in the Cedar River from 1979 to 1985 had a viral prevalence exceeding 90% (Mulcahy et al. 1983b; Mulcahy et al. 1987). We found sockeye salmon had an IHNV prevalence of about 90% in 1986. The virus levels detected in Cedar River water by direct plaque assay in our experiments were approximately 0.7 PFU·mL^{-1} (Table 3). Leong and Turner (1979) reported an IHNV titer of 400 PFU·mL^{-1} in water released from incubator trays containing juvenile steelhead (*Oncorhynchus mykiss*) undergoing an IHN epizootic at the Round Butte Hatchery.

The combination of TFF and PEG precipitation enabled us to isolate IHN virus from the water sample collected below the Landsburg Dam pipeline crossing on the Cedar River. After TFF of the downstream sample, the level of virus in the retentate was 19.5 PFU·mL^{-1} and in the filtrate solution it was below detection limits. The pellet from PEG precipitation of the retentate contained 1200 PFU·g^{-1}. These results indicate that about 900 infectious particles of IHNV were in the 10-L water sample collected downstream from the weir. No virus was detected in the upstream sample. Sockeye salmon were observed below the weir, but not above, and we estimated that 10 to 15 adult fish were in a direct line between the pipeline crossing and the sampling point. Tissue and fluid samples of adult sockeye salmon collected nearby at the time the water samples were taken yielded a 95% incidence of IHNV infection. The occurrence of detectable levels of IHNV below the pipeline, and the absence of virus above, strongly suggests that the infected adult sockeye salmon were an important source of virus for infection of other susceptible fish downstream.

Virus was isolated from the 10-L water sample obtained from the adult holding pond at the Leavenworth National Fish Hatchery. Tangential flow filtration resulted in a retentate containing a 15-fold increase in IHNV titer. Alone, TFF recovered 42% of the available virus (Table 4). Further concentration by PEG-20 000 resulted in a 32% overall recovery and a 2113-fold increase in titer. No virus was detected in the PEG pellet of either filtrate solutions. The positive control showed virus recoveries of 139% for the retentate and 61% for the pellet (Table 4). Virus in the water sample from the adult holding pond and the control sample could be detected by direct plating, and precipitation by PEG resulted in a 149 and 159-fold titer increase for hatchery water sample and control water, respectively. The prevalence of IHNV-infected ripe females at the hatchery was 35% on the date when the water sample was col-

lected. Virus isolates from the water samples and from spawning females were confirmed as IHNV by serum neutralization (Amos 1985).

Practical Uses of these Techniques

The epizootiology of IHNV is not completely understood. However, the most important mechanism for transmission appears to be from infected fish to susceptible fish through the water (Wingfield and Chan 1970; Mulcahy et al. 1983a). The concentration methods in this study could be used to determine the minimum level of IHNV necessary to initiate viral infections in various species of fish. Also, the virus level could be tested in rivers at different dates before, during, and after spawning migration of salmonids, or on the same day at different locations along the river.

Our techniques could be used to determine IHNV titers at several points in a hatchery at selected times of the year or at intervals during routine operations to determine the effect of hatchery practices and design on IHNV transmission. Watanabe et al. (1988) used TFF to quantify IHNV titers in water samples from two sources at the Round Butte Hatchery in Oregon. Holding ponds containing adult steelhead had 1 PFU·5 mL^{-1} and circular tanks containing steelhead fry undergoing a chronic IHNV mortality had titers of 1 PFU·50 mL^{-1}. Our results and those of LaPatra et al. (1987) indicated that the crowding of infected adult salmon can greatly increase the IHNV titer of holding areas and suggested that hatchery operations may need to be modified to reduce the opportunity for transmission of the virus.

Treatment of hatchery water supplies by ozone or ultraviolet irradiation has been proposed as a method for control of IHN. The methods presented in this paper could be used to confirm IHNV was present in the water supply before expensive treatment devices are installed. In addition, the techniques could be used to compare the effects of hatchery practices on the levels of IHNV in different parts of the facility. Various pond designs, water flow rates, and effluent treatment systems could be evaluated. Also, the IHNV titers in ponds containing different stocks or species at various rearing densities could be compared. The methods used in this study to concentrate IHNV should be appropriate for detection of low levels of other fish rhabdoviruses.

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Identification of Spring- and Autumn-Spawning Herring (*Clupea harengus harengus*) using Maturity Stages Assigned from a Gonadosomatic Index Model

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A model is developed to identify the spawning type of individual herring (*Clupea harengus harengus*) from the sympatric spring and autumn spawning stocks in the southern Gulf of St. Lawrence (NAFO Division 4T). The maturity stage is assigned from a gonadosomatic index model using discriminant analysis and the spawning type is determined from the maturity stage and the month of capture according to a detailed description of the annual maturity cycle of each type. The model is shown to be objective, quantitative, and precise. Greater than 97% overall agreement was achieved between the spawning type classification of individuals by histological means and by the model, significantly improving the identification accuracy compared with a macroscopic maturity stage key. The model also has the advantages of (1) identifying the spawning type directly by determining the "season of spawning" rather than the "season spawned" as is inferred from indirect evidence such as otolith characteristics or meristic data, (2) requiring easily obtained, quantifiable data, and (3) enabling the rapid treatment of a large number of specimens.

Un modèle est développé pour l'identification du groupe reproducteur des individus des stocks sympatriques de printemps et d'automne du hareng (*Clupea harengus harengus*) du sud du golfe St.-Laurent (division 4T de l'OPANO). Le stade de maturité est déterminé en premier lieu à partir d'un rapport gonadosomatique par l'analyse discriminante. Le groupe reproducteur est déterminé en second lieu à partir du stade de maturité et le mois de capture selon une description détaillée du cycle reproducteur annuel de chaque groupe. Il est démontré que ce modèle est objectif, quantitatif et précis. Une concordance totale de plus de 97% a été atteinte entre la classification des groupes reproducteurs déterminés par les moyens histologiques et par le modèle, améliorant significativement le précision d'identification par rapport à l'utilisation d'une clé macroscopique des stades de maturité. Ce modèle possède également les avantages suivants: (1) l'identification directe du groupe reproducteur en déterminant "la saison actuelle de la fraie" plutôt que "la saison de naissance" comme les évidences indirectes telles que les caractéristiques des otolithes ou les données méristiques l'indiquent, (2) la facilité d'obtenir les données quantifiables requises, et (3) la rapidité du traitement d'un grand nombre d'individus.

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Fisheries researchers have long recognized the existence of spring- and autumn-spawning herring (*Clupea harengus harengus*) within various population complexes in the northwest Atlantic (Jean 1953; Day 1957) distinguished by numerous biological and behavioural characteristics (Messieh and Tibbo 1971; Parsons and Hodder 1971). Although the actual biological link between these seasonal spawning types is still the topic of active debate (Smith and Jamieson 1986), investigations throughout the 1960's and 1970's in the Gulf of St. Lawrence led fisheries managers to consider the two spawning types within each population complex as separate unit stocks for assessment and management purposes (e.g. McQuinn 1988; Chadwick and Cairns 1988). However, sympatric spring- and autumn-spawners often intermingle in feeding and overwintering areas and are caught in mixed commercial fisheries. The accuracy of stock assessments based on separate virtual population analyses for each spawning type depends upon the precision with which individual fish, sampled from the commercial catches, are assigned to each type.

Many techniques have been employed to differentiate between spring- and autumn-spawners, either on a stock or an individual basis. At the stock level, methods include the statistical comparison of meristic and morphometric characters, fecundities, and more recently, allelic frequencies using electrophoretic techniques (Parsons and Hodder 1971; Messieh and Tibbo 1971; Baxter 1959; Kornfield et al. 1982). Most of these studies have demonstrated statistical differences in the chosen characteristics between the two spawning types. However, either the practical constraints of the techniques or large overlaps in the frequency distributions of the measured parameters has prevented accurate spawning type identifications of individual fish by these methods.

Otolith morphometry (Messieh 1972) and discriminant analyses of meristic data (Parsons 1972; Messieh 1975) have been used to classify individual fish as spring- or autumn-spawners. However, a large number of meristic variables are required for significant discrimination, restricting the usefulness of this technique for the routine analysis of commercial data. More

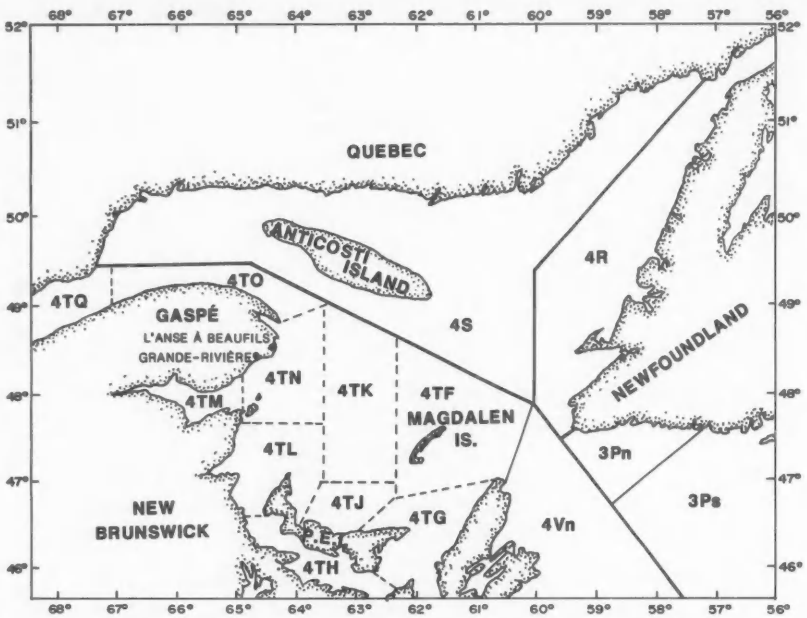

FIG. 1. Gulf of St. Lawrence showing unit areas in NAFO Division 4T and sampling sites.

importantly, no definite link has yet been demonstrated between the intraspecific variations of meristic or morphometric characters and differences in the genomes of herring stocks, while the effects of environmental factors on the modification of these characters has been well documented (Buckmann and Parrish 1958; Parrish and Sharman 1958; Ihssen et al. 1981; Ryman and Stahl 1981). In addition, these characters have been shown to reflect environmental conditions at hatching. Consequently, the above techniques only infer spawning season indirectly by assuming that herring spawn at the same time of the year that they were hatched. This assumption has yet to be substantiated.

Maturity stages have been used routinely over the past few decades to assign individual herring caught in the northwest Atlantic to one or the other spawning type. This method was based on the observation that peak spawning for each type within a population complex is restricted to a relatively fixed and discrete period. In the southern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization Division 4T), peak spawning for spring spawners occurs from May to early June, and for autumn spawners from mid-August to September, although limited spawning has been reported throughout the summer months and in October (see Haegele and Schweigert 1985). The spawning type of an individual herring is assigned by identifying its maturity stage from the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) maturity stage key (a variation of the maturity stage key adopted by the International Council for the Exploration of the Sea Herring Committee (Parrish and Saville 1965)) and determining the most probable spawning season given the month of capture (Cleary et al. 1982). For example, a stage V (mature) individual caught in April would be classified as a spring-spawner, whereas a stage VIII (beginning of maturation) would be an autumn-spawner. In July, the stage V would be an autumn-spawner and the stage VIII a spring-spawner. Since only limited spawning occurs in late June and July, herring which spawn before June 30 are designated spring-spawners, while after the first of July they are considered autumn-spawners.

The maturity stage method has the advantages of (1) identifying the spawning type from direct evidence, i.e. estimating when a fish had or would have spawned according to the reproductive cycle of each type, and (2) being relatively rapid, enabling the routine examination of a large number of specimens. However, despite these advantages, and the ease of determining the spawning type of mature fish caught at the peak of the spawning seasons, the gonadal development schedules of northwest Atlantic herring stocks have not been sufficiently well described to reliably determine the spawning type of nonspawning fish at other times of the year. In addition, maturity stage identification using the CAFSAC maturity stage key involves a subjective assessment of gonad appearance, especially at the beginning or gametogenesis, and the key is designed for use on fresh specimens. Several criteria, such as gonad colour, are unreliable for use with frozen samples (Cleary et al. 1982; Landry and McQuinn 1988).

Faced with the subjectivity involved in determining maturity stages from macroscopic staging keys, several authors have suggested that a method based on a function of gonad weight would be more accurate and quantifiable for assessing gonadal development (Scott 1979; Idler et al. 1981; Hay 1985). Gonadosomatic indices (GSI) have been used to model gonadal development in several teleosts (Delahunty and deVlaming 1980; deVlaming et al. 1982) including Pacific herring (*Clupea harengus pallasi*) (Hay 1985).

The present study describes a procedure which assigns the maturity stage of individual herring from a GSI model. The model was developed from a database in which the maturity stages were assigned histologically. Although too laborious for routine use, histological techniques are clearly superior to macroscopic examination for assessing gonadal development (Scott 1979; Delahunty and deVlaming 1980). The model will be

TABLE 1. Histological criteria for the classification of herring maturity stages (from Landry and McQuinn 1988).

Sex	State of Maturity	Stage	Description
Male	Virgin	I	Organization of connective tissue and blood vessel system; division of primary germ-cells to produce first group of spermatogonia, which remain few in number. Connective tissue not yet structured into seminiferous tubules.
	Beginning of maturation phase	IIa	Spermatogenesis begins; level of maturation does not exceed spermatogonia multiplication phase. Distinguished from stage I by presence of larger quantity of spermatogonia.
		IIb	Spermatogonia proceed to other phases of spermatogenetic cycle. End of stage IIb: testis contain all maturation phases of germinal cells (primary germ-cells, spermatogonia, primary and secondary spermatocytes, spermatids and spermatozoa); a few spermatozoa found only in a few tubules.
	Rapid growth phase	III	Spermatozoa in majority of tubule lumina. Proportion of spermatozoa does not exceed one-third volume of lumina.
		IV	Proportion of spermatozoa between one-third and three-fifths of volume of lumina.
		V	Beginning of stage V: thin band of spermatocytes may still be found along periphery of tubules; later, only spermatozoa attached to Sertoli cells are found, distributed in bundles throughout lumina. End of stage V: spermatozoa detached from Sertoli cells, distributed uniformly throughout lumina.
	Spawning	VI	Sperm separated from tubule walls and typically absent from several tubules.
	Beginning of reconstitution phase	VII	Majority of tubules empty of sperm. Small groups of primary germ-cells are identifiable in a few tubules. Distinguished from stage I by presence of spawning residue.
	Beginning of new maturation phase	VIIIa	Primary germ-cells continue divisions to produce spermatogonia, which undergo multiplication phase and become prominent in testis.
		VIIIb	All developmental phases of germ-cells present; spermatozoa few in number and found only in a few tubules.
			Stage VIII distinguished from stage II by presence of spawning residue. Development proceeds to stage III.
Female	Virgin	I	Organization of connective tissue and blood vessel system; division of ovogonia producing first generation of ovocytes. Ovocytes dark, do not contain yolk, have not begun maturation phase. Theca only follicular layer present. Lamellar structure of ovary obvious in longitudinal section.
	Beginning of maturation phase	IIa	Ovocyte cytoplasm becomes more pale than in stage I, followed by production of yolk vesicles around cell periphery.
		IIb	First yolk globules appear around ovocyte periphery but remain few in number.
	Rapid growth phase	IIIa	Yolk globules occupy up to one-half of cytoplasm around cell periphery.
		IIIb	Yolk globules occupy all of cytoplasm but are detached from the nuclear membrane.
		IV	Yolk globules pressed against nuclear membrane; at times infiltrated into nucleus; yolk vesicles form only a thin band around the cell periphery.
		V	Decentralization of nucleus followed by complete disappearance; yolk globules become voluminous (by fusion); ovocytes still encased by follicules.
	Spawning	VI	Empty follicules around periphery of ovary (ovulation), compressed by ovulated eggs situated in center; egg abundance varies according to advancement of spawning.
	Beginning of reconstitution phase	VII	Immature ovocytes as in stage I; distinguished from stage I by presence of spawning residue; remaining mature eggs in resorption.
	Beginning of newmaturation phase	VIIIa	Ovocyte cytoplasm has become pale but does not yet contain yolk.
		VIIIb	York vesicle production phase.
		VIIIc	Appearance of first yolk globules around ovocyte periphery but few in number.
			Stage VIII distinguished from stage II by presence of spawning residue. Ovary then develops to stage III.

TABLE 2. Test for regression parallelism of gonad weight on somatic weight among herring maturity stages (sexes combined).

Source of variation	*SS*	*df*	*MS*	*F*	*P*
Model	1156 593.80	23	50 286.69	407.1	<0.001
Somatic weight	168 557.42	1	168 557.42	1364.5	<0.001
Maturity stage	854 019.51	11	77 638.14	628.5	<0.001
Interaction	134 016.87	11	12 183.45	98.6	<0.001
Residual	253 366.78	2051	123.53		
Total	1409 960.58	2074	679.83		

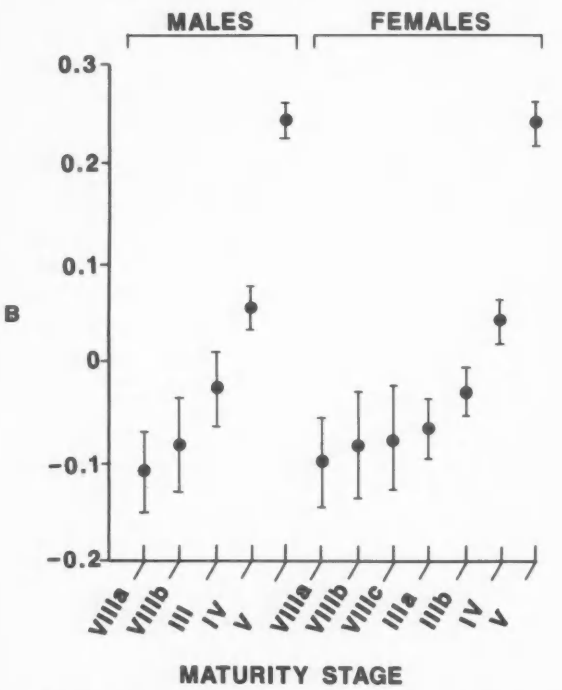

FIG. 2. Standardized slopes (B) with 95% confidence intervals estimated from the test of regression parallelism for gonad weight on somatic weight for maturity stages VIIIa to V for male and female herring in NAFO Division 4T.

compared with the maturity stage key presently used for most northwest Atlantic herring stocks by (1) testing the accuracy of the maturity stage assignments of both the GSI model and the CAFSAC staging key relative to assignments using histological criteria and (2) comparing the spawning type classification percentages resulting from the GSI model and CAFSAC maturity stage assignments. The histological maturity stage and spawning type classifications are assumed to be without error for the following analyses.

Materials and Methods

Histological Maturity Stage Classification

Spring- and autumn-spawning herring were sampled from the Baie des Chaleurs commercial gillnet fishery in 1984 (Grande-Rivière and Anse-à-Beaufils, Fig. 1). Each week, from the beginning of May to mid-October, a sample of approximately 100 fresh herring stratified by 20-mm length intervals was collected, from which standard biological data (total length, weight, gonad weight, and stage of sexual maturity from visual examination) and otoliths were obtained. A gonad section was taken from each individual, fixed in Bouin's solution for 16–24 hr and preserved in 70% alcohol. The 2149 sections thus obtained were stained in hematoxylin and eosin, and set in paraffin blocks from which 6- to 7-μm slices were cut and mounted on glass microscope slides.

The gonads were classified into eight stages of sexual maturity according to the histological criteria of Landry and McQuinn (1988). The histological stages (Table 1) were defined so that the corresponding macroscopic appearance of the gonads of each stage coincided as closely as possible with the CAFSAC maturity stage key (Cleary et al. 1982). As the macroscopic separation of stages III and VIII from the CAFSAC key has often proven difficult, special emphasis was placed on the description of these stages in the histological staging key. These stages were subdivided into IIIa and b, and VIIIa, b, and c for the females and VIIIa and b for the males to permit a more detailed delineation of the maturation process during this phase of development. Because the spawning type of immature fish (stages I and II) could not be determined with certainty from their gonadal development, these individuals were excluded from the following analyses.

Gonadosomatic Index Model

Estimating maturity stages from a GSI assumes that gonad weight increases with sexual development. The principal change occurring as the ovaries mature is an increase in the size of the oocytes (Landry and McQuinn 1988), first due to changes within the nucleus, followed by the production and accumulation of yolk vesicles and globules (Holliday 1960; deVlaming 1983). In the maturing testes, there is a continuous progression from the production of spermatocytes, to spermatids and finally to spermatozoa (Bowers and Holliday 1961). These processes result in an increase in gonadal weight from stage VIIIa to stage V.

Stages VI and VII are characterized respectively by the shedding of gametes during spawning, and the beginning of the reconstructive processes within the gonads which includes the resorption of unshed mature eggs and sperm (Landry and McQuinn 1988). Clearly, the gonad weights of these two stages could not be used as a measure of gonadal development comparable with stages VIIIa through V. Consequently, these stages have been excluded from the gonadosomatic index model.

When classifying maturity stages from a GSI, the index must be calculated to be independent of body size. This assumes that the slope of the linear arithmetic relationship between gonad weight and the measure of body size is constant for different stages of gonadal development (deVlaming et al. 1982). The GSI is most commonly expressed as a percentage of body size,

$$\text{GSI} = (W_G/S_B)\cdot 100$$

where W_G is gonad weight (grams) and S_B is a measure of body size, either total weight (grams), somatic weight (grams) or the allometric equivalent of total weight (length cubed). A comparison of the regression lines of W_G on somatic weight revealed that the slopes (B) were significantly different ($P<0.001$) among the various maturity stages (Table 2) and in fact, exhibited an exponential relationship with advancing gonadal development (Fig. 2). However, a log–log transformation of gonad weight versus total length yielded linear relationships where the

TABLE 3. (A) Test for regression parallelism of ln gonad weight on ln total length among herring maturity stages, and (B) analysis of covariance for the final regression model yielding the pooled regression coefficient (sexes combined).

Source of variation	*SS*	*df*	*MS*	*F*	*P*
(A)					
Model	2360.8527	23	102.6458	712.5706	<0.001
Log total length	181.0264	1	181.0264	1256.6919	<0.001
Maturity stage	2177.6498	11	197.9682	1374.3019	<0.001
Interaction	2.1765	11	0.1978	1.3736	0.178
Residual	295.4465	2051	0.1440		
Total	2656.2992	2074	1.2808		
(B)					
Model	2358.6762	12	196.5564	1361.7871	<0.001
Log total length	181.0264	1	181.0264	1254.1924	<0.001
Maturity stage	2177.6498	11	197.9682	1371.5685	<0.001
Residual	297.6230	2062	0.1443		
Total	2656.2992	2074	1.2808		

Pooled regression coefficient = 5.3342, $r^2 = 0.89$

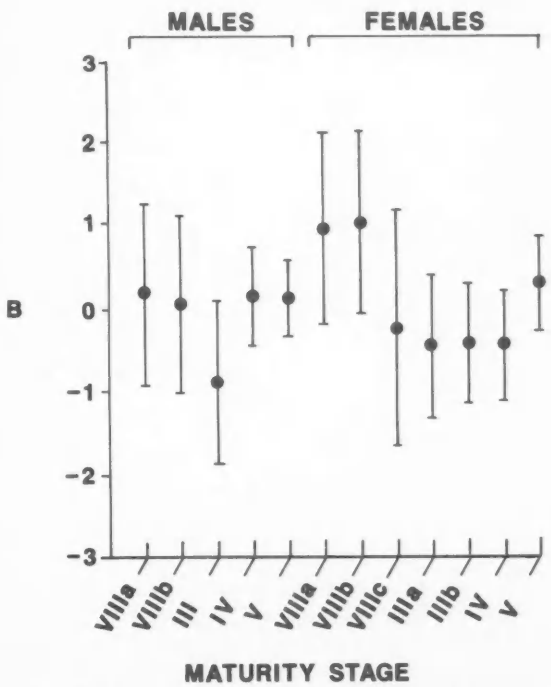

FIG. 3. Standardized slopes (B) with 95% confidence intervals estimated from the test of regression parallelism for ln gonad weight on ln total length for maturity stages VIIIa to V for male and female herring in NAFO Division 4T.

slopes were not significantly different from the common slope ($P>0.1$) and therefore were independent of maturity stage (Table 3a, Fig. 3). The GSI was thus expressed as a power function of total length,

$$(1)\quad \mathrm{GSI} = (W_G/L_T^{5.334})\cdot 10^{14}$$

where W_G is fresh gonad weight (grams), L_T is fresh total length (millimetres), 5.334 is the empirically fitted pooled regression coefficient of ln W_G versus ln L_T derived from an ANCOVA (Table 3b), and the multiplier is simply a scaling factor.

Discriminant analyses were then conducted to delineate the histological maturity stages on the basis of the GSI distributions of each stage. A ln transformation was performed on the GSI to normalize the data and to reduce the heterogeneity of the intergroup variances. The analyses produced a classification function for each maturity stage (Table 4) from which a score or probability of membership to a given stage was calculated. The stage-specific classification function yielding the highest score indicated the most probable maturity stage. The cutoff points between adjacent maturity stages could then be determined from these functions. The accuracy of the discriminant analysis in determining the histological maturity stages was evaluated by reclassifying each individual using the leave-one-out or "jackknife" method (Lachenbruch and Mickey 1968) which yields "an almost unbiased estimate of the expected actual error rate" (Lachenbruch 1975).

Maturation Schedules

The histological data were also used to describe the gonadal development schedules of spring- and autumn-spawning herring in the southern Gulf of St. Lawrence. Although the sexes are often treated together in herring maturity studies, the physiological processes occurring within the gonads during maturation are obviously very different and the staging schemes are based on different criteria (Landry and McQuinn 1988). Consequently, sex-specific maturation schedules were determined for both spawning types in the southern Gulf between May and October by plotting the frequency distribution of the histological maturity stages and delineating between the stocks by following the monthly progression of these distributions (Fig. 4a,b).

Although the delineations between the distributions were made subjectively, the spawning type assignment from the maturity stages was for the most part straightforward. For example, in the month of May, maturing, spawning, and spent herring (stages IV, V, VI, and VII) were spring-spawners, while herring at the beginning of maturation (stage VIII and III) were autumn-spawners (Fig. 4a,b). However, in certain instances it

TABLE 4. Stage- and sex-specific discriminant functions, with means and 95% confidence intervals, used to identify the most probable maturity stage for herring from the gonadosomatic index.

Sex	Stage	Discriminant function	Mean	C.I.
Male	VIIIa	−12.5272 + 10.5693 ln(GSI)	2.0659	±0.6267
	VIIIb	−22.1991 + 14.5146 ln(GSI)	2.8371	±0.8969
	III	−47.8517 + 21.7520 ln(GSI)	4.2518	±1.3476
	IV	−62.6929 + 25.0000 ln(GSI)	4.8867	±1.1442
	V	−75.9540 + 27.5806 ln(GSI)	5.3911	±0.5375
Female	VIIIa	−35.1198 + 27.6296 ln(GSI)	2.4013	±0.3224
	VIIIb	−46.7958 + 32.1261 ln(GSI)	2.7921	±0.6037
	VIIIc	−58.5124 + 36.0792 ln(GSI)	3.1357	±0.4286
	IIIa	−72.8554 + 40.3952 ln(GSI)	3.5108	±0.4980
	IIIb	−96.1815 + 46.5677 ln(GSI)	4.0472	±0.6068
	IV	−143.508 + 57.0757 ln(GSI)	4.9605	±0.7047
	V	−168.567 + 61.9216 ln(GSI)	5.3817	±0.4948

was difficult to assess from the maturity stage assignment alone whether individuals found within stages at the extremes of the distributions of each spawning type belonged to one type or the other, e.g. maturing (stage IV) herring in September. Fish in these stages could have been either advanced members of one type or slower developing individuals of the other. For these individuals, the histological sections were reexamined to determine whether the gonads were at the beginning of that stage of development or near the end. The fish were then allocated to either the more advanced or less advanced spawning type according to their development.

Although the histological data covered the major sexual development periods of both spawning types (May–October), these data were available for only a portion of one year and were restricted to a small area of the southern Gulf. A more extensive data set was needed to better define the annual maturity cycle of each type over time and over the spatial distribution of the two stocks. Interannual or spatial variation in maturation rates would prevent the application of single maturity schedule based on one year of data to other years and areas.

The GSI was calculated from equation (1) for all commercial sampling data (37 547 individuals) available from NAFO Division 4T (unit areas 4TF, 4TG, 4TH, 4TL, 4TM, 4TN, and 4TO) between 1970 and 1984 (Fig. 1). Since the exponent in equation (1) was estimated from fresh samples, length and gonad weight were converted to the fresh condition for all frozen samples used in the GSI calculations. The GSI distributions were plotted by month and sex, with the limits of the modeled maturity stages, derived from the discriminant analyses, subsequently superimposed (Fig. 5). These GSI distributions were subsequently used to fine tune the delineation of the range of maturity stages occupied by each spawning type in each month and, in conjunction with the histological maturity stage distributions, gave a detailed view of their annual maturity cycles.

Spawning Type Classification

A computerized procedure was developed from the discriminant functions and the maturation schedules to classify the spawning type of each individual from the histological data. The procedure consisted of determining the most probable maturity stage of each fish from the discriminant functions, and then using the month of capture and the maturity cycles to identify its spawning type. As was noted earlier, there were months when specimens from both spawning types could be found in the same stage of maturity. In these cases, the spawning type was assigned by identifying the discriminant function with the second highest score, indicating whether that individual was closer to the next more advanced stage or to the preceding stage. This enabled the further subdivision of each maturity stage into an early and an advanced phase from the GSI.

Results

Maturity Stage Assignment

The ability of the discriminant functions and the CAFSAC maturity stage key to assign the histologically defined maturity stages is compared in Tables 5 and 6. A direct comparison was not possible for the substages, as stages VIII and III could not be subdivided using the CAFSAC key. Therefore the discriminant function classification percentages were also calculated with the substages combined. Nine of 12 stages showed equal or significantly higher percentages of correct classification (test of percentages, Sokal and Rohlf 1969) using the discriminant functions. This improvement was most evident for stages VIII and III, which are particularly difficult to identify using the CAFSAC key (Cleary et al. 1982). Overall, the discriminant functions yielded mean correct classifications of 75.3 and 83.9% for males and females, respectively, compared with 62.6 and 65.5% for the CAFSAC key.

Spawning Type Identification

Clearly, the precision of the spawning type identifications depends upon the precision of the delineations between the maturity stages of each type. The historical GSI distributions (Fig. 5) showed that on a monthly scale, the interannual maturation rates of the two spawning types were indeed consistent over the 15 yr of data, the distributions of each stock being well defined and quite distinct in most months. Errors would occur where the tails of the distributions overlapped, although this would involve relatively few individuals.

In the month of June, however, a monthly definition did not give sufficient resolution to delineate the GSI distributions. Male autumn-spawners, for example, which were found mostly in stage VIII in May, developed quickly through the month of June, to be found in stages IV and V in July. Due to this rapid gonadal development, the distributions of the two spawning types became more easily discernible when the data were presented separately for the first and second halves of the month.

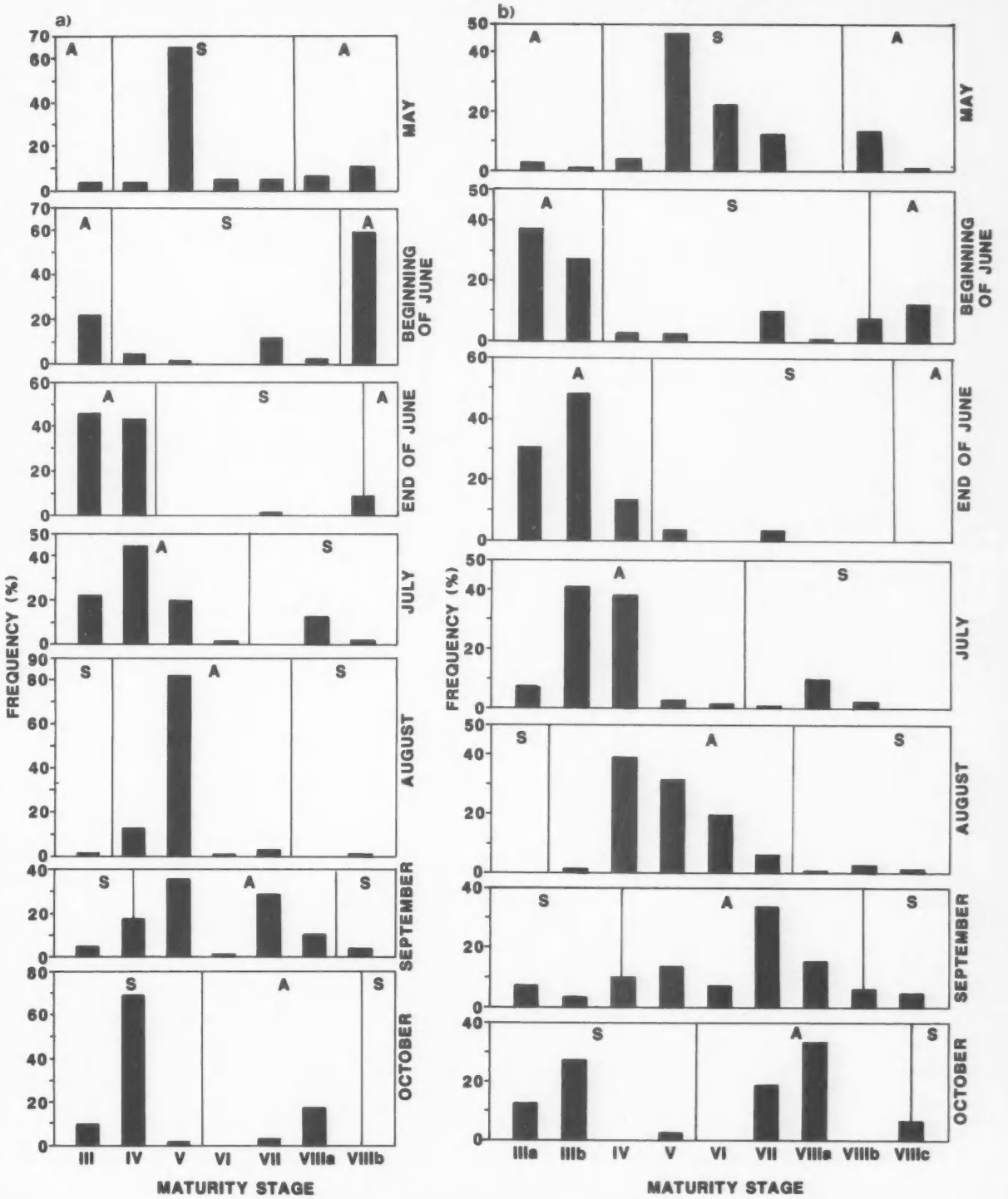

FIG. 4. (a) Frequency distributions of histologically determined male maturity stages by month. (b) Frequency distributions of histologically determined female maturity stages by month. Vertical lines delineate spring (S) and autumn (A) spawning herring.

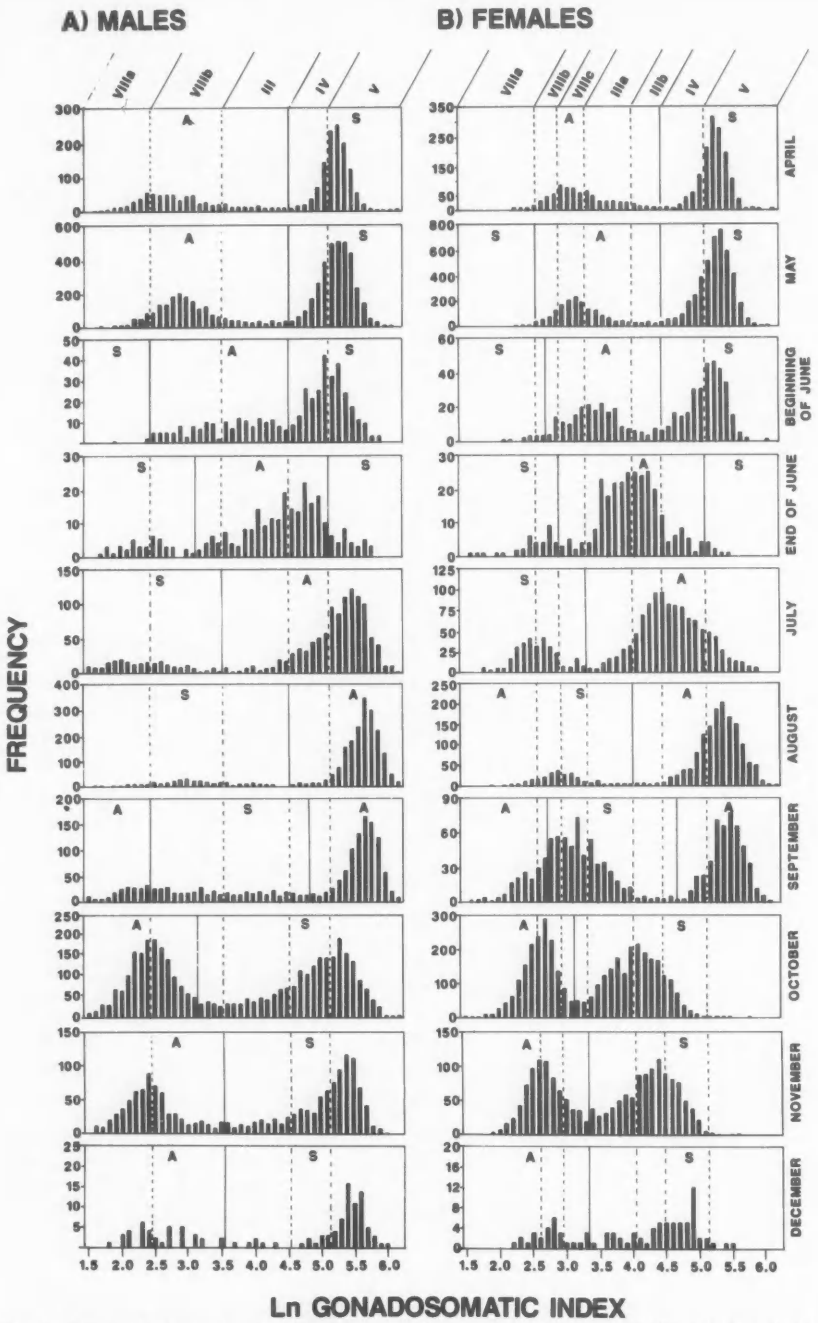

FIG. 5. GSI distributions of spring (S) and autumn (A) spawning herring in NAFO Division 4T by month and sex from samples collected between 1970 and 1984. Broken lines delineate maturity stages VIIIa to V and solid lines delineate spawning types.

By following the progression of the distributions, it is evident that at the beginning of June, there remained some spring-spawners in advanced stage IV and stage V, while the autumn-spawners were in the latter phase of stage VIIIb and in stage III. By the end of the month, the autumn-spawners had reached stage IV while a few stage V spring-spawners were still apparent, and would presumably spawn before the end of the month.

The delineation between the GSI distributions was also difficult in the month of September. This difficulty underlined the importance of correctly identifying all spent fish (stage VII)

TABLE 5. Classification percentages of histologically determined maturity stages by the discriminant functions and the CAFSAC maturity stage key for male herring. Probabilities (*P*) refer to differences between percent classification of underlined values (test of percentages).

		Discriminant functions						CAFSAC key				
Histology	(*n*)	VIIIa	VIIIb	(VIII)	III	IV	V	VIII	III	IV	V	*P*
VIIIa	(73)	84.9	15.1	(100.0)	0.0	0.0	0.0	74.0	26.0	0.0	0.0	<0.001
VIIIb	(101)	17.8	77.7	(95.0)	5.0	0.0	0.0	36.5	63.5	0.0	0.0	<0.001
III	(121)	0.0	14.9	(14.9)	57.0	9.1	19.0	5.0	42.1	51.2	1.7	0.020
IV	(253)	0.0	2.4	(2.4)	22.1	39.9	35.6	0.0	15.7	62.3	22.0	<0.001
V	(460)	0.0	0.0	(0.0)	0.7	14.6	84.8	0.0	0.0	1.5	98.3	<0.001

TABLE 6. Classification percentages of histologically determined maturity stages by the discriminant functions and the CAFSAC maturity stage key for female herring. Probabilities (*P*) refer to differences between percent classification of underlined values (test of percentages).

		Discriminant functions								CAFSAC key				
Histology	(*n*)	VIIIa	VIIIb	VIIIc	(VIII)	IIIa	IIIb	(III)	IV	V	VIII	III	IV	V	*P*
VIIIa	(53)	92.2	7.8	0.0	(100.0)	0.0	0.0	(0.0)	0.0	0.0	98.1	1.9	0.0	0.0	n.s.
VIIIb	(59)	24.1	44.8	29.3	(98.3)	1.7	0.0	(1.7)	0.0	0.0	59.3	40.7	0.0	0.0	<0.001
VIIIc	(33)	0.0	21.9	56.3	(78.2)	21.8	0.0	(21.8)	0.0	0.0	51.5	48.5	0.0	0.0	0.018
IIIa	(109)	0.0	0.9	19.2	(21.1)	66.1	13.8	(79.9)	0.0	0.0	19.3	77.1	3.7	0.0	n.s.
IIIb	(200)	0.0	0.0	0.0	(0.0)	16.5	76.5	(93.0)	7.0	0.0	3.0	52.2	44.8	0.0	<0.001
IV	(270)	0.0	0.0	0.0	(0.0)	0.0	11.5	(11.5)	56.3	32.2	0.0	1.5	84.8	13.7	<0.001
V	(229)	0.0	0.0	0.0	(0.0)	0.0	0.9	(0.9)	17.4	81.7	0.0	0.0	64.2	35.8	<0.001

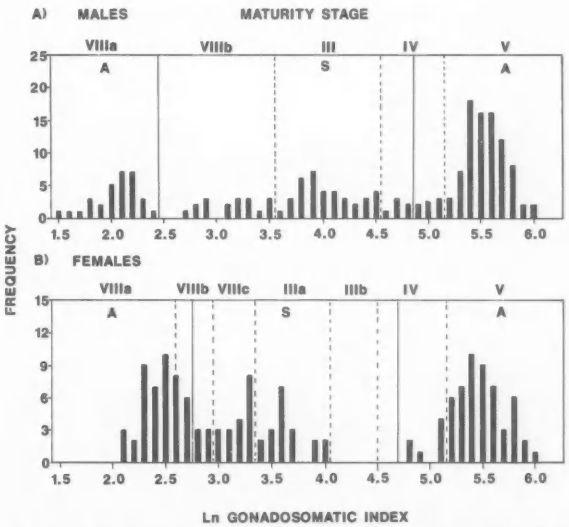

FIG. 6. GSI distributions of spring (S) and autumn (A) spawning herring in NAFO Division 4T by sex for histological samples collected in September, 1984. Broken lines delineate maturity stages VIIIa to V and solid lines delineate spawning types.

during the routine collection of biological data. Although the early phase of this stage is relatively easy to identify macroscopically, advanced stage VII gonads can be difficult to distinguish from stage VIII, especially from frozen samples. Individuals misclassified as stage VIII would be included in the GSI model but, due to the presence of unresorbed residue from the recent spawn, the GSI would suggest a more advanced state of development, leading possibly to an incorrect spawning type classification. This can be illustrated by comparing the GSI distributions of the early developmental stages from the commercial data (Fig. 5) with the histological data (Fig. 6) for the month of September. The separation between the spring- and autumn-spawners (e.g. male stage VIIIa and stage VIIIb) was much clearer from the histological data where all stage VII fish were removed. The overall error associated with misclassified stage VII fish should however be small, as this problem is mainly restricted to a relatively short period immediately following peak spawning activity (June and September). Moreover, recent improvements to the macroscopic classification criteria (Landry and McQuinn 1988) should facilitate the future identification of this stage.

Several interesting features were noted from the maturity stage and GSI distributions. Fig. 4a and b revealed that the majority of spent herring remained in stage VII in the month following peak spawning (June and September) before beginning a new maturation cycle. The maturity cycle chart in Cleary et al. (1982) had assumed that development to stage VIII after spawning was more rapid and therefore the majority of stage VIII herring in May–June and August–September were recently spawned individuals. Figs. 4 and 5 also confirmed that little spawning occurred in late-June and July, suggesting that the July 1 separation date between the two spawning seasons was appropriate. Also, autumn-spawning was essentially finished by October, as very few females were found in stage V or VI in this month, the stage V males being spring-spawners which had matured more quickly than the females. In fact, the gonadal development of the males was generally more advanced than that of the females throughout the development cycle, supporting similar observations in other Atlantic and Pacific herring populations (Parsons and Hodder 1975; Hay 1985). Holliday (1962) found that even in hermaphrodite herring, the maturity stage of the testis was more advanced than that of the ovary.

Spawning Type Classification

Sex-specific maturity cycle charts (Table 7) summarize the spawning type classifications given the month and maturity

TABLE 7. Classification of spring (S) and autumn (A) spawning herring by maturity stage and month as determined by histological maturity stages and GSI distributions for male and female herring. Horizontal lines delineate spawning types.

Sex	Maturity stage	Month											
		Jan.	Feb.	Mar.	Apr.	May	Beginning Jun.	End Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Male	III	S	S	S	A	A	A	A	A	S	S	S	S	S
	IV	S	S	S	S	S	S	A	A	A	-S/A-	S	S	S
	V	S	S	S	S	S	S	S	A	A	A	S	S	S
	VI	S	S	S	S	S	S	S	A	A	A	A	A	A
	VII	A	S	S	S	S	S	S	S	A	A	A	A	A
	VIIIa	A	A	A	A	A	S	S	S	S	A	A	A	A
	VIIIb	A	A	A	A	A	A	-S/A-	S	S	S	-A/S-	A	A
Female	IIIa	S	S	A	A	A	A	A	A	S	S	S	S	S
	IIIb	S	S	S	A	A	A	A	A	A	S	S	S	S
	IV	S	S	S	S	S	S	A	A	A	-S/A-	S	S	S
	V	S	S	S	S	S	S	S	A	A	A	S	S	S
	VI	S	S	S	S	S	S	S	A	A	A	A	A	A
	VII	A	S	S	S	S	S	S	S	A	A	A	A	A
	VIIIa	A	A	A	A	S	S	S	S	A	A	A	A	A
	VIIIb	A	A	A	A	A	-S/A-	S	S	S	-A/S-	A	A	A
	VIIIc	A	A	A	A	A	A	A	S	S	S	-A/S-	A	A

TABLE 8. Classification percentages of histologically determined herring spawning types by the discriminant functions and the CAFSAC maturity stage key by month and sex. Probabilities (*P*) refer to differences between the two methods in the percent classification of spring- and autumn-spawners combined. Sample sizes are in parentheses.

Sex	Month	Discriminant functions			CAFSAC key			*P*
		Spring	Autumn	Combined	Spring	Autumn	Combined	
Male	May	88.5 (182)	100.0 (41)	90.6	83.3 (186)	88.1 (42)	84.9	0.039
	June	100.0 (10)	95.9 (122)	96.2	20.0 (10)	87.2 (125)	82.2	<0.001
	July	100.0 (30)	100.0 (196)	100.0	100.0 (32)	100.0 (199)	100.0	n.s.
	August	100.0 (4)	100.0 (245)	100.0	100.0 (4)	100.0 (245)	100.0	n.s.
	September	93.4 (61)	100.0 (102)	97.5	82.3 (62)	98.0 (102)	92.1	0.023
	October	100.0 (51)	100.0 (11)	100.0	100.0 (51)	100.0 (11)	100.0	n.s.
Female	May	97.9 (140)	93.8 (32)	97.1	85.1 (141)	96.9 (32)	87.3	0.003
	June	100.0 (17)	98.0 (153)	98.2	29.4 (17)	97.4 (153)	90.6	0.001
	July	100.0 (31)	100.0 (254)	100.0	94.1 (34)	100.0 (254)	99.3	0.047
	August	100.0 (11)	100.0 (218)	100.0	100.0 (11)	99.1 (218)	98.7	0.046
	September	85.7 (49)	100.0 (80)	94.6	100.0 (50)	72.5 (80)	83.1	0.002
	October	86.4 (22)	95.5 (22)	90.9	81.8 (22)	95.5 (22)	88.6	n.s.

stage. The maturity cycle was interpolated between January and March as no samples were available. A comparison of the GSI distributions in December and April indicated that little gonadal development occurred during these winter months.

Classification of the males to the histologically determined spawning types using the GSI model and Table 7 ranged from 88.5 to 100% by month for spring-spawners and 95.9 to 100% for autumn-spawners, with correct classifications of 92.6 and 99.3% for spring- and autumn-spawners, respectively (Table 8). For the females, correct classifications ranged from 85.7 to 100% by month for spring-spawners and 93.8 to 100% for autumn-spawners, with 95.2 and 99.2% for spring- and autumn-spawners, respectively. The overall efficiency of the model was 93.8 and 99.3% for spring- and autumn-spawners, respectively. In comparison, spawning type classification using the CAFSAC maturity key and Table 7 ranged from 20.0 to 100% by month, with an overall efficiency of 85.6 and 96.4% for spring- and autumn-spawners, respectively. The discriminant functions yielded significantly higher classification percentages in most months (test of percentages, Sokal and Rohlf 1969) but particularly in June and September, mainly due to the inability of the CAFSAC key to subdivide maturity stages VIII and III.

Discussion

The development of methods for the identification of seasonal spawning types in mixed herring fisheries has been the subject of numerous scientific studies involving stocks on both sides of the Atlantic. Most methods have used indirect evidence based on meristic and morphometric differences found among various herring stocks. However, these methods have achieved only limited success in assigning individuals to the proper spawning type, as error rates using various meristic characters have been in the range of 20 to 30% (Parsons 1972; Messieh 1975) when compared with the visual maturity stage method. Mature, ripe, and running fish were often assigned to the non-spawning type. These indirect methods all assumed a high degree of discreteness between the types at the time of the for-

mation of these characters (during the larval or early juvenile phase) and continued discreteness throughout their reproductive life histories (during spawning). Several studies have shown evidence questioning the reproductive discreteness of these seasonal spawning types (Einarsson 1958; Anokhina 1971; Grant 1984; Aneer 1985; King 1985; Smith and Jamieson 1986). The relatively high disagreement between the spawning type classification of herring identified by meristics and by maturity stages strongly suggests that reproductive isolation is not complete.

The state of sexual maturity can be used to determine the spawning type of individuals directly, and makes no assumption about their reproductive isolation. Obviously, a herring spawning in May is a spring spawner, regardless of the season hatched. The major deficiency of maturity stage methods has been the high subjectivity and variability in assigning the maturity stages from the macroscopic examination of gonads, especially at the beginning of gametogenesis (stages VIII and III) (Cleary et al. 1982). Landry and McQuinn (1988) showed that macroscopic maturity stage keys were, at times, vague in their descriptions and used several highly subjective criteria. Clearly, a method of determining maturity stages based on a function of gonad weight is more objective and quantifiable, eliminating much of the variability associated with the visual method.

The present study described a gonadosomatic index model which significantly improved the identification of histologically determined maturity stages compared with the macroscopic staging key presently employed. This improvement was especially evident during the early phase of maturation where several stages could be subdivided by the GSI model. It must also be pointed out that the macroscopic staging for the present study was performed by an experienced biologist on fresh samples from which the macroscopic determination of maturity stages is considerably easier than from frozen specimens (Cleary et al. 1982). This is not the usual situation, as there are often many people with varying degrees of expertise involved in assigning maturity stages, and samples are almost always frozen. Thus, in this comparison the macroscopic classification rates reflect the best obtainable results. Misclassification percentages would increase considerably using visual staging keys on frozen samples while the GSI model would be unaffected assuming the proper conversions are made from frozen to fresh measurements.

Significantly higher spawning type classification percentages were achieved using the GSI model compared with the CAFSAC maturity stage key, resulting in a 97.7% overall agreement between the histologically determined spawning types and those identified by the model (using stages VIIIa through V). The ability of the GSI model to subdivide stages VIII and III contributed largely to this higher precision. In those months when both spawning types were found in the same macroscopic stage of development (Table 7), significant classification errors were introduced by the visual method (Table 8). In addition, where the GSI distributions of the two types were found within the same histological maturity stage, the second discriminant function was used to further subdivide these maturity stages, enabling an even finer separation.

Although stages VI and VII must still be determined macroscopically, this should not introduce a major source of error. Stage VI females were correctly identified 81% of the time. Even if certain stage VI individuals are misclassified as a stage V, as often happened with the males (53%), in most cases the spawning type would be the same. However, particular care must be taken to correctly identify stage VII macroscopically, as the spawning type could be misidentified if these individuals are included in the GSI model.

Finally, one of the most important advantages of determining maturity stages from the GSI model is the ability to rapidly identify the spawning type of individuals from historical data. The basic data required for the model (gonad weight, total length, and date of capture) have been routinely collected for most northwest Atlantic herring stocks for several decades. This assumes, of course, that the maturity cycle chart defined for a given stock is applicable over the historical time period. The interannual consistency of the gonadal development cycles, as illustrated by the distinct GSI distributions of each stock over 15 yr of commercial data (Fig. 5), supports this assumption. Furthermore, studies have shown that the annual spawning period of various herring stocks has been extremely regular, at least on the monthly scale considered here, varying by only a couple of weeks over many decades of observation (Jean 1956; Iles 1964; Cushing 1969; Messieh and Tibbo 1971).

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Temporal and Spatial Patterns of Porewater Phosphorus in Shallow Sediments, and its Potential Transport into Narrow Lake, Alberta

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Shaw, J. F. H., and E. E. Prepas. 1989. Temporal and spatial patterns of porewater phosphorus in shallow sediments, and its potential transport into Narrow Lake, Alberta. Can. J. Fish. Aquat. Sci. 46: 981–988.

During 1985 and 1986, summer and spatial patterns of porewater soluble reactive phosphorus (SRP) from sediments ≤15-m depth were examined at Narrow Lake, a deep, mesoeutrophic Albertan lake. At three sites (different in depth and macrophyte colonization), trends in porewater SRP concentrations ([SRP]) in the top 5 cm of the sediment from May to August varied, possibly due to root uptake of SRP by macrophytes. At a depth of 5 m, mean (in the top 5 cm of the sediment) and variance of porewater [SRP] at one site (<0.15 m^2) were the same as over the entire lake. Excluding data from macrophyte sites, porewater [SRP] were positively related to depth of the water column ($P<0.0001$). Molecular diffusion of SRP from sediments with and without macrophytes located in the trophogenic zone was calculated. During summer, molecular diffusion from shallow sediments to the trophogenic zone was 0.05 $mg \cdot m^{-2} \cdot d^{-1}$, or 29% of atmospheric deposition of phosphorus (P) (the major external source of P to the lake). A sampling strategy is discussed to enable the calculation of whole-lake P transport from shallow sediments to the trophogenic zone in lakes with similar morphometry and trophic status to Narrow Lake.

En 1985 et 1986, des profils estivaux et spatiaux du phosphore réactif soluble dans l'eau interstitielle provenant des sédiments se trouvant à une profondeur égale ou inférieure à 15 m ont été étudiés au lac Narrow, lac profond mésotrophe de l'Alberta. À trois endroits (de profondeur différente et différent par la colonisation par les macrophytes), les tendances des concentrations de phosphore réactif soluble dans l'eau interstitielle dans les 5 premiers centimètres de sédiment variaient de mai à août, probablement à cause de l'absorption du phosphore réactif soluble par les racines des macrophytes. À une profondeur de 5 m, la moyenne (dans les cinq premiers centimètre de sédiments) et la variance de la concentration de phosphore réactif soluble dans l'eau interstitielle à un endroit (inférieur à 0,15 m^2) avaient la même valeur que pour l'ensemble du lac. En excluant les données provenant des endroits où poussaient des macrophytes, la concentration de phosphore réactif soluble dans l'eau interstitielle était liée de façon positive à la profondeur de la colonne d'eau (p inférieure à 0,0001). On a calculé la diffusion moléculaire du phosphore réactif soluble des sédiments avec et sans macrophytes se trouvant dans la zone trophogène. En été, la diffusion moléculaire des sédiments peu profonds vers la zone trophogène était de 0,05 $mg \cdot m^{-2}$ par jour ou 29 % du dépôt atmosphérique de P (la principale source extérieure de P du lac). Une stratégie d'échantillonnage est étudiée pour permettre de calculer le transport du phosphore à l'échelle du lac à partir de sédiments peu profonds vers la zone trophogène dans des lacs présentant une morphométrie et un état trophique similaires à ceux du lac Narrow.

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Phosphorus (P) is the major limiting nutrient for algal productivity in many freshwater lakes (Schindler 1977). Phosphorus can be released from lake sediments into anaerobic lakewater (e.g. Einsele 1936, 1938; Ohle 1937; Einsele and Vetter 1938; Mortimer 1941, 1942; Nurnberg 1984; Riley and Prepas 1984), or into aerobic lakewater at high temperature and neutral to basic pH (Andersen 1975; Banoub 1975; Kamp-Nielsen 1975; Lee et al. 1977; Rippey 1977; Ku et al. 1978; Ulen 1978; Holdren and Armstrong 1980). In thermally stratified lakes, sediment P release during summer into anaerobic (hypolimnetic) lakewater is easier to quantify than release into aerobic (trophogenic) lakewater. Phosphorus, released into an anaerobic hypolimnion, accumulates below the thermocline. Transport of P from the hypolimnion into the epilimnion occurs only when the thermocline erodes (Quay et al. 1980; Schindler et al. 1980; Kortmann et al. 1982; Stauffer and Armstrong 1984) or when the P gradient across the thermocline is large (Imboden and Emerson 1978). Thus, little of the P released from hypolimnetic sediments is available to algae during summer stratification. This release can be estimated from changes in hypolimnetic P mass over time.

In contrast, relatively little is known about sediment P release from shallow sediments (i.e. those sediments located in the trophogenic zone) into aerobic lakewater. Since the trophogenic zone usually contains a much larger volume of water than the hypolimnion, P released from shallow sediments is diluted more than P released from hypolimnetic sediments. Phosphorus released from these shallow sediments does not remain in solution in the trophogenic zone of P-limited lakes; it is taken up by algae, cycled through other trophic levels, and removed from the trophogenic zone by sedimentation. An increase of P in the trophogenic zone may also be caused by allochtonous P inputs. Thus, an increase in trophogenic P due to release from shallow sediments is difficult to quantify.

Release of P from shallow sediments into aerobic lakewater has been estimated either from P budgets or from core incu-

bations and porewater samples. Estimates of sediment P release calculated as the residual in a P budget include the compounded error of other parameters in the budget. Incubations of cores in the laboratory oversimplify sediment–lake systems by failing to include important factors such as bioturbation, mixing, and groundwater flow (e.g. Gallepp 1979; Holdren and Armstrong 1980; Van Liere and Mur 1982). In situ estimates of P release have been based on gradients of porewater P, which is the most mobile form of P in the sediment (Syers et al. 1973; Bostrom et al. 1982). These rates are likely underestimates of P release because: (1) P gradients near the sediment–water interface may be steeper than between the top 3 cm of the sediment and the overlying water, and (2) P transport by bioturbation and mixing may be greater than by molecular diffusion. In addition, these estimates of sediment P release are based on a single collection of porewater (Bannerman et al. 1974; Quigley and Robbins 1986). Porewater P concentrations can vary over spring and the open water season, within one depth, with lake depth, and with macrophyte colonization (Bannerman et al. 1974; Holdren et al. 1977; Carignan 1984a, 1985; Carignan and Nriagu 1985; Kawai et al. 1985; Smith and Adams 1986; Drake and Heany 1987). However, these studies provided only limited information on seasonal and spatial patterns of porewater P in lakes during summer. Thus, it is difficult to calculate a "whole-lake" sediment P release rate into aerobic lakewater.

During 1985 and 1986, we collected porewater and lakewater samples near the sediment–water interface at Narrow Lake, a deep mesoeutrophic lake in Alberta. The variability of porewater P concentrations in shallow sediments was examined with depth in the sediment, at sites with and without macrophytes, from May to August, within a single depth over the entire lake, and between depths. We used these results to calculate potential P release from shallow sediments into the trophogenic zone during the summer, and to outline strategies for sampling porewater P at other lakes.

Materials and Methods

Study Area

Narrow Lake is located in central Alberta (54°35′N, 113°37′W) in the mixed-wood section of the boreal forest (Strong and Leggat 1981). Drift, primarily glacial till interbedded with alluvial deposits, surrounds the lake. Sedimentary bedrock lies 5 to 10 m underneath the deepest part of the lake (Green 1972; Kjearsgaard 1972). Narrow lake is a small, relatively deep, mesoeutrophic lake (surface area 1.1 km^2, maximum depth 36 m, and average summer trophogenic total P concentration 11 $mg \cdot m^{-3}$). The bottom of the trophogenic zone, defined as the depth to 1% of surface penetrating irradiance, was at 12 m during the summers of 1985 and 1986 (A. M. Trimbee and E. E. Prepas, unpubl. data). The thermocline was at 6-m depth during the summers of 1985 and 1986. Since most algae (determined as chlorophyll *a* concentration per cubic metre) were below the epilimnion (Prepas and Trew 1983), P release into trophogenic lakewater from sediments below the thermocline could affect algal biomass. Therefore, shallow sediments were defined as those that extended from the lake shore to the bottom of the trophogenic zone. Shallow sediments represented 47% of the surface area of the lake. Aquatic macrophytes were restricted to the littoral zone, less than 15–16% of the lake surface area. The maximum depth of macrophyte colonization was between 5 and 6 m; however, most macrophytes were found between 0 and 3-m depths.

Porewater Collection and Analyses

Sediment porewater was collected in situ with Plexiglass peepers, fitted with Gelman HT-450 membrane filters, from May to August in 1985 and 1986. Peepers used in 1985 had 140 chambers, spaced 1 cm apart, in two columns (Hesslein 1976). Smaller peepers with 25 chambers per side, spaced 1 cm apart, were used in 1986 and were especially useful in shallow, sandy sediments.

Peepers were prepared as outlined in Carignan (1984b) with the following modification: peepers were transported from the lab to the lake wrapped in two plastic bags, both of which were flushed with N_2 to remove O_2, purged and filled with N_2 to keep O_2 out. The peepers were placed in the lake sediment and retrieved by SCUBA divers. Five to 10 chambers were left above the sediment–water interface to equilibrate with lakewater immediately above the sediments. Water in the peeper chambers was withdrawn with syringes within 5 to 10 min of peeper retrieval and placed in prepared serum vials. Vials were prewashed in 3% HCl, washed with double distilled water (DDW), and dried; in a glovebag, they were flushed and filled with N_2, and capped with Wheaton stoppers. The pressure in the vials was maintained from the time water samples were injected into the vials until the samples were analyzed. Therefore, we assume that diffusion of gases through the stoppers was minimal. Peepers and porewater samples were handled in a N_2 environment to reduce loss of dissolved P by chemical precipitation caused by changes in redox potential (Bray et al. 1973; Troup et al. 1974).

Because the peepers had chambers in two columns, water samples from both sides of the peeper were analyzed separately; thus, duplicate P profiles were obtained for each peeper. The volume required for porewater analyses was 6 mL. Since each chamber contained about 3 mL, it was necessary to pool samples from adjacent chambers below the sediment–water interface. The samples above the sediment–water interface were more dilute than porewater; water from all chambers above the sediment–water interface were pooled. Unless otherwise indicated, the following samples were collected per side: (1) one lakewater sample pooled from all chambers above the sediment–water interface, (2) five porewater samples from 0 to 10 cm in the sediment at 2-cm intervals, and (3) nine porewater samples from 10 to 55 cm in the sediment at 5-cm intervals for the long peepers or one sample from 10 to 15 cm in the sediment for the small peepers.

Porewater and lakewater from the serum vials were subsampled within 2 h after collection, diluted 5 to 25 times with DDW, and analyzed for SRP within 12 h after collection (Murphy and Riley 1962). Samples from five peepers were also analyzed for total dissolved P (TDP); concentrations of SRP were 94 to 100% of TDP. Since the difference between SRP and TDP concentrations was small, samples were routinely analyzed according to the less time consuming SRP analyses. All peeper and sample preparation as well as chemical analyses were performed at the Meanook Biological Research Station, located 15 km from Narrow Lake.

Evaluation of Porewater Collection and Analysis

Peepers were placed at depths of 4 and 15 m in one transect (A in Fig. 1) during May 1985 to determine the time required

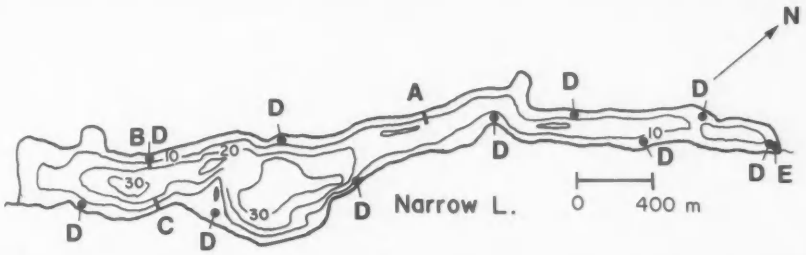


FIG. 1. Peeper locations at Narrow Lake in 1985 and 1986. Peeper transects are indicated as A, B, and C, peeper sites at 5-m lake depth as D, and shallow site without macrophytes as E.

for peeper equilibration (i.e. time when P concentrations within peepers were equal to those in porewater). Peepers were retrieved after 1, 3, 6, 9, 11, 17, 25, and 31 d at the 4-m site and after 6, 13, 14, 24, and 27 d at the 15-m site. For each site, comparisons between porewater [SRP] after different installation times were nonorthogonal; therefore, ANOVAs were performed with different probabilities than for orthogonal comparisons (i.e. experimentwise error rate *a*; Sokal and Rohlf 1981, p. 242). First, [SRP] from consecutive dates were compared; the equilibration time was chosen as the number of days after which [SRP] remained the same. Two additional nonorthogonal comparisons were performed to determine whether [SRP] were (1) significantly less before equilibration time and (2) similar after equilibration time, relative to those at the equilibration time.

To determine the effect of sampling delay on porewater [SRP], a 0.5-mL sample was removed from each chamber of a peeper at four time intervals (0, 10, 20, and 30 min after retrieval); the peeper was equilibrated at a 7.5-m depth and collected in August 1986. Porewater was pooled from 5-cm sections of the peeper to obtain an adequate aliquot for SRP analyses. Samples were placed directly into culture tubes for subsequent analyses. These samples were also used to test differences in porewater [SRP] between the two sides of the peeper. The comparisons of [SRP] after different time intervals were nonorthogonal; concentrations after different sampling delays were compared as for peeper equilibration time.

To test the effect of laboratory subsampling and dilutions on porewater [SRP], porewater was retrieved from 15-m depth on two separate occasions in 1985. Twenty milligrams P per cubic metre was added to culture tubes with porewater aliquots, and [SRP] between tubes with and without P additions were compared.

Temporal and Spatial Variability of Porewater SRP

To examine temporal changes in porewater [SRP], porewater samples were collected every second week from May to August 1986. At least one peeper was installed at three sites (Fig. 1): one shallow (2.5 m) with macrophytes (*Vallisneria* sp) and one deep (7.5 m), both located on transect A, and one shallow without macrophytes (3 m, site E).

To determine spatial variability in porewater [SRP], 15 peepers were placed at 11 sites, all at 5-m depths. Five peepers were placed close together (<0.15 m^2) on transect A (Fig. 1), while one peeper was placed at each of 10 additional sites (D, Fig. 1). These sites were equidistant along the length of Narrow Lake, alternating on east and west shores. To minimize the impact of temporal changes on porewater [SRP], all 15 peepers were retrieved and analyzed on August 14 and 15, 1986. Porewater [SRP] from the five peepers on transect A were also used to test normality and homogeneity of sample variance.

To investigate variability of porewater [SRP] with lake depth, one peeper each was placed at 3-, 7-, 10-, and 15-m depths along three transects. The transects covered both sides and basins of Narrow Lake and were perpendicular to the shore (A, B, and C, Fig. 1). Peepers were installed in each of the three transects, two or three times over the summer of 1985. In addition, peepers were installed at 4-m depths in transect A, 5 times during 1985. Peepers were also installed in transect A during the summer of 1986 at the following depths: (1) 2.5, 5, 7.5, and 10 m (twice) and (2) 1, 2.5, 4, 5, 6, 7.5, 9, 10, and 11 m (once). In total, porewater [SRP] were determined from 44 peepers from these three transects: 28 and 16 peepers in 1985 and 1986, respectively. Of 28 peepers sampled in 1985, 18 were located in shallow sediments; all peepers in 1986 were located in shallow sediments.

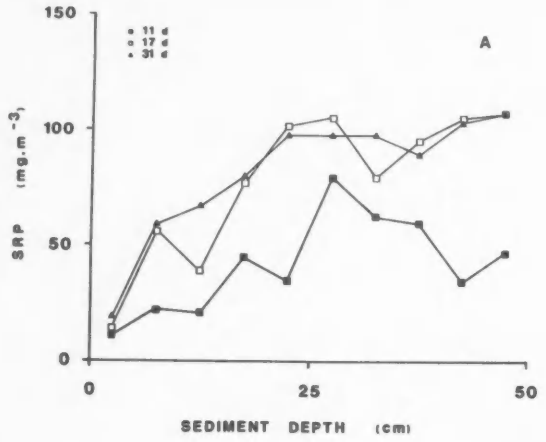
Statistical tests were performed according to Sokal and Rohlf (1981) and Snedecor and Cochran (1980). Differences in porewater [SRP] over the summer and with depth of the water column were determined on porewater in the top 15 and 5 cm of the sediment, respectively. Concentrations in the top 5 cm of the sediment were calculated as a weighted average of three samples from the top 6 cm in the sediment. This stratum was chosen because it was within the most active layer contributing P to the overlying water, i.e. the top 10 cm of the sediment (Tessenow 1972; Schindler et al. 1977). Deeper sections were analyzed to determine a potential source of P to the top 5-cm section.

SRP Release from Shallow Sediments into Lakewater

Molecular diffusion of SRP across the sediment–water interface was calculated according to equation (1) (Berner 1980):

$$(1) \quad J = \phi \cdot D \cdot \theta^{-2} \cdot dC/dx,$$

in which J is the SRP flux across the sediment–water interface, ϕ is the water content by volume (0.57; J. F. H. Shaw unpubl. data), D is the molecular diffusion coefficient (1.24×10^{-9} m$^2 \cdot$s^{-1}; Quigley and Robbins 1986), θ^2 is the tortuosity term ($\phi^{-0.8}$; Berner 1980), and dC/dx is the SRP gradient across the sediment–water interface. SRP gradients were calculated between [SRP] in the top 5 cm of the sediment and the overlying lakewater at sites from transects A, B, and C (Fig. 1). Concentrations of SRP 0.5 cm above the sediment–water interface were assumed to equal [SRP] measured from 0 to 10 cm above the interface. To calculate J, shallow sediments were divided in a 0–3 m depth stratum (where macrophytes were



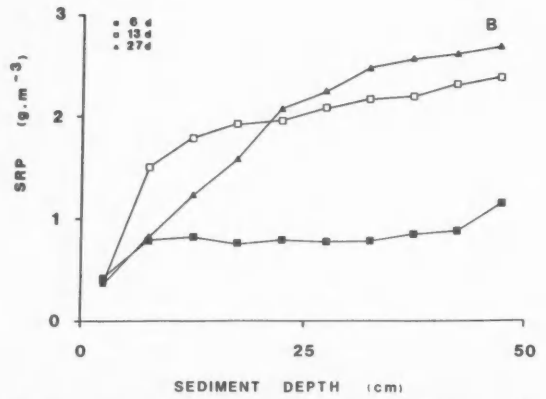


FIG. 2. Porewater soluble reactive phosphorus (SRP) in the top 50 cm of the sediment at 4-m depth (*a*) and 15-m depth (*b*) after different incubation periods in the sediment.

abundant) and a 3–12 m stratum (where macrophytes were scarce or absent). Average SRP gradients were calculated for each stratum and pooled, weighted for sediment area.

Results

Evaluation of Porewater Collection and Analysis

Equilibration time for [SRP] in the peepers was determined at two sites, 4 and 15 m. At the 4-m depth, porewater [SRP] in the top 50 cm of the sediment increased during the first 17 d and did not change during the subsequent 14 d (nonorthogonal comparisons; $a<0.01$ and >0.1, respectively). The average porewater [SRP] in the top 50 cm of the sediment was 42 $mg \cdot m^{-3}$ after 11 d, increased to 78 $mg \cdot m^{-3}$ after 17 d, and remained similar, at 72 $mg \cdot m^{-3}$, after 31 d (Fig. 2a). At the 15-m site, porewater [SRP] increased significantly from 6 to 13 d and did not change significantly from 13 to 31 d ($a<0.01$ and >0.1, respectively). The average porewater [SRP] in the top 50 cm of the sediment at 5-m depth was 815 $mg \cdot m^{-3}$ after 6 d, increased to 1890 $mg \cdot m^{-3}$ after 13 d, and remained unchanged at 1883 $mg \cdot m^{-3}$ after 31 d (Fig. 2b). Equilibration time (17 and 13 d at 4- and 15-m depth, respectively) differed only by 4 d between the two sites; both were well within the range of 3 to 20 d determined by Carignan (1984b, 1985). Consequently, all peepers at Narrow Lake were equilibrated in the sediment for a minimum of 2 wk before they were sampled.

We determined the effect of sampling delay (0, 10, 20, and 30 min) on porewater [SRP] from a peeper installed at a 7.5-m depth. [SRP] in porewater and in lakewater just above the sediment–water interface from the two sides were not significantly different (paired *t*-test; $P>0.2$; data from four different time periods and four depths in the sediment were included in the analysis). Therefore, [SRP] from two sides of the peeper were pooled. The pooled porewater [SRP] tended to decrease over 30 min (on average 8%); the decrease was significant (2-way ANOVA; $P<0.05$). Porewater [SRP] did not differ between 0 and 10 min after peeper retrieval (nonorthogonal comparisons; $a>0.05$). Porewater [SRP] were significantly less after 20 and 30 min compared with 0 min after peeper retrieval from the sediment ($a<0.025$). Subsampling of the peepers (except the deepest 30 cm of the large peepers) was completed within 5 to 10 min of retrieval from lake sediments; these porewater [SRP] were not affected by a delay in sampling.

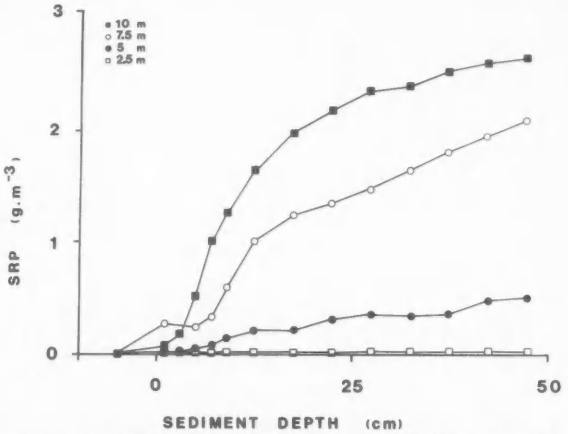


FIG. 3. Porewater soluble reactive phosphorus (SRP) in the top 50 cm of the sediment from four lake depths collected on July 24–25, 1985.

TABLE 1. Mean, range, and SD of soluble reactive phosphorus concentrations (SRP, in milligrams per cubic metre) in lakewater just above the sediment–water interface (−10–0 cm) and in porewater from the top 15 cm of the sediment from a lake depth of 5 m at Narrow Lake collected in August 1986.

	SRP					
Depth in the sediment (cm)	Within 0.15 m^2 ($n=5$)			Entire lake ($n=10$)		
	Mean	Range	SD	Mean	Range	SD
−10–0	3	2–4	1.1	3	1–5	1.3
0–2	41	20–85	25.5	49	7–150	47.0
2–4	71	41–137	39.8	137	13–368	104.2
4–6	106	48–223	70.3	176	32–522	144.3
6–8	107	61–196	53.9	192	51–576	153.4
8–10	112	78–186	45.3	202	54–538	134.5
10–15	121	69–195	49.6	202	44–509	125.0

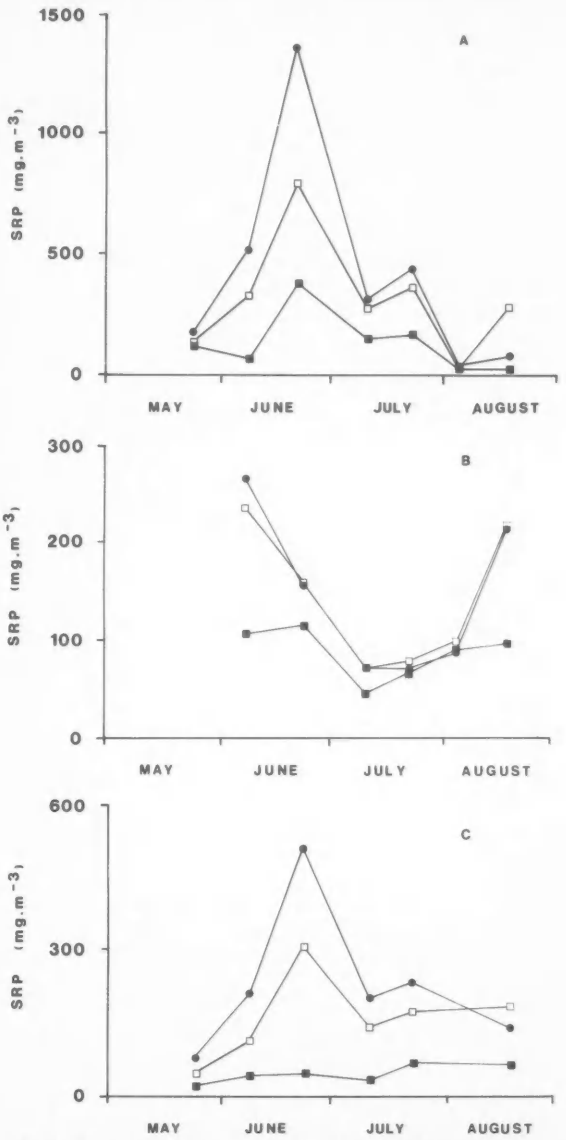


FIG. 4. Porewater soluble reactive phosphorus (SRP) over the summer of 1986: (*a*) a shallow site with macrophytes, (*b*) a shallow site without macropyhtes, and (*c*) a deep site. Porewater SRP concentrations from three sediment sections: 0 to 5 cm (■), 5 to 10 cm (□), and 10 to 15 cm in the sediment (●).

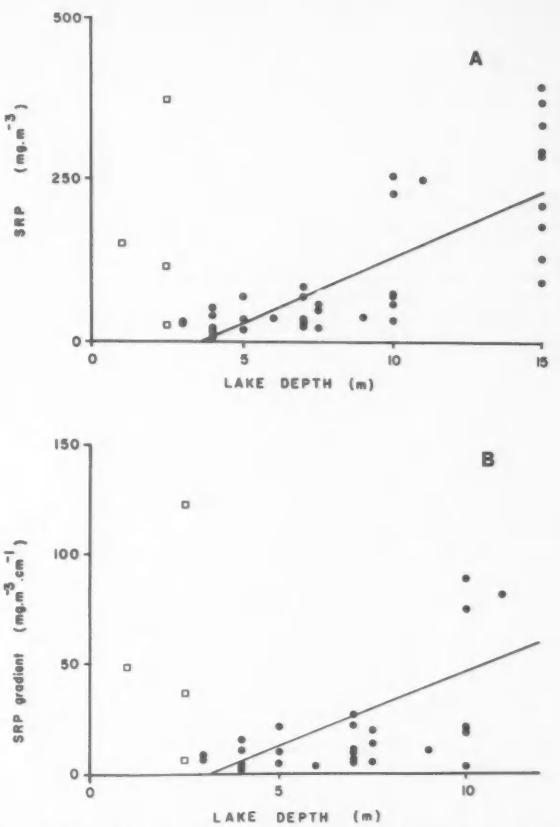


FIG. 5. Relationships between (*a*) average porewater soluble reactive phosphorus (SRP) in the top 5 cm of the sediment, and (*b*) SRP gradients across the sediment–water interface and lake depth (in metres) at Narrow Lake. Regression lines were calculated with all data collected in transects during 1985 and 1986 excluding sites colonized by macrophytes (□).

The recovery of 20 $mg \cdot m^{-3}$ standard P additions was not affected by subsampling and dilutions in both peepers (paired *t*-tests difference = 20 mg $P \cdot m^{-3}$; $P>0.2$ and 0.1, respectively).

Porewater [SRP] increased with depth in the sediment in 52 of 71 peepers collected at Narrow Lake during 1985 and 1986 (all equilibrated peepers: paired *t*-test, $P<0.025$, Fig. 3). Therefore, depth in the sediment was treated as a block in subsequent analyses of spatial and seasonal variability of [SRP]. [SRP] were similar for both sides of 51 of these 71 peepers ($P>0.025$). Average [SRP] of the two sides were used in further analyses to reduce the variability of the SRP data (unless otherwise indicated).

In 1986, normality of porewater [SRP] and homogeneity of variance were evaluated with five peepers spaced close together (0.15 m^2) at 5-m depths (transect A, Fig. 1). To increase the sample size, data from two sides of the peeper were analyzed separately. The average [SRP] in lakewater just above the sediment–water interface was 3 $mg \cdot m^{-3}$. Porewater [SRP] increased from 41 $mg \cdot m^{-3}$ in the top 2 cm of the sediment to 121 $mg \cdot m^{-3}$, 10 to 15 cm below the sediment–water interface. Porewater [SRP] varied by three- to four-fold within each sediment depth (Table 1). When [SRP] in lakewater just above the sediment–water interface and in porewater from each sediment depth were tested for normality, five of seven sections followed a normal distribution (above the sediment–water interface, and 0–2, 4–6, 6–8, 10–15 cm in the sediment; Kolmogorov–Smirnov test, $P>0.1$). [SRP] in the other two sections (2–4 and 8–10 cm in the sediment) were slightly different from a normal distribution ($0.05>P>0.01$). Overall, variance of porewater [SRP] from the small site was homogeneous (F_{max} test, $P>0.05$).

In summary, porewater [SRP] equilibrated within 2 wk after installation of the peeper. [SRP] in this equilibrated porewater

were not affected by: (1) sampling delay of 10 min (after retrieval from the bottom sediments) and (2) subsampling and diluting for chemical analyses. In addition, porewater [SRP] met two important conditions for parametric statistical analyses: normality and homogeneity of variance.

Temporal and Spatial Variability of Porewater SRP

Comparisons of porewater [SRP] in the top 15 cm of the sediment at three sites (shallow with macrophytes, shallow without macrophytes, and deep) showed significant temporal changes from mid-May to mid-August 1986 (two-way ANOVA; $P<0.01$). At the shallow site with macrophytes (2.5 m transect A), porewater [SRP] in the top 5 cm of the sediment first increased from May to June and then decreased after June 22, 1986 (Fig. 4). In contrast, porewater [SRP] at the shallow site without macrophytes (site E) increased during June, decreased from June to July, and then increased after July 11, 1986 (Fig. 4). Porewater [SRP] decreased from May to June and increased from June to August at the deep site (7.5 m transect A; Fig. 4). At all three sites, temporal changes in porewater [SRP] at depths greater than 5 cm below the sediment–water interface were similar to the trends observed for the top 5 cm in the sediment (Fig. 4).

Average porewater [SRP] in the top 15 cm of the sediment were lower at one site (transect A, Fig. 1; 99 $mg \cdot m^{-3}$) than at 10 other sites over the entire lake (D, Fig. 1; 168 $mg \cdot m^{-3}$). Porewater [SRP] from each section in the sediment were also significantly lower in peepers placed close together than those placed over the entire lake (two-way ANOVA; $P<0.005$). Although SD of porewater [SRP] within each sediment depth was lower in the small site than over the entire lake (Table 1), overall variance was not significantly different (two-level nested ANOVA with unequal sample size, within and between sites as groups, and depth in the sediment as subgroups; $P>0.05$).

Porewater [SRP] in the top 5 cm of the sediment increased with depth of the water column (Fig. 5a). Porewater [SRP] in macrophyte sites were much greater than those at sites without macrophytes; data from the macrophyte sites were excluded in the following analyses. A highly significant relationship was found between porewater [SRP] and depth (Fig. 5a; $r^2=0.63$, $P<0.0001$). The relationship between porewater [SRP] in shallow sediments and depth was also significant ($r^2=0.37$, $P<0.001$).

SRP Release from Shallow Sediments into Lakewater

At sites less than 12-m depth located in transects, [SRP] in lakewater above the sediment–water interface varied from 1 to 14 $mg \cdot m^{-3}$. Porewater [SRP] in the top 5 cm of the sediments varied from 5 to 374 $mg \cdot m^{-3}$ and was, on average, 13 times greater than [SRP] in lakewater just above the sediment–water interface. When sites colonized by macrophytes were excluded, SRP gradients across the sediment–water interface increased with depth (Fig. 5b; $r^2=0.33$, $P<0.001$); the average SRP gradient according to this relationship for depths from 3 to 12 m was 22.4 $mg \cdot m^{-3} \cdot cm^{-1}$. At sites colonized by macrophytes (depths from 0 to 3 m), the average SRP gradient across the sediment–water interface was 53.3 $mg \cdot m^{-3} \cdot cm^{-1}$. Overall, the average SRP gradient across the sediment–water interface of shallow sediments was 28.8 $mg \cdot m^{-3} \cdot cm^{-1}$; SRP release from shallow sediments to lakewater by molecular diffusion was 0.11 $mg \cdot m^{-2} \cdot d^{-1}$.

Discussion

To date, there is little information on variation in porewater [SRP] over the summer, within a single depth, and between depths in one lake. Observations of seasonal trends in porewater [SRP] during spring and the open water season are limited to lakes where porewater was collected once per month and mostly from sites colonized by macrophytes (Holdren et al. 1977; Carignan 1985; Smith and Adams 1986).

At Narrow Lake, porewater [SRP] in the top 5 cm of the sediment first increased and then decreased over the summer at a shallow site with macrophytes. Porewater [SRP] at a macrophyte site in Lake Wingra (a shallow, eutrophic lake) decreased and then increased over the summer (Smith and Adams 1986). In contrast, porewater [SRP] in a macrophyte bed at Lake Memphremagog (a large mesotrophic lake) did not change over the summer in the top 5 cm of the sediment, but appeared to decrease from 5 to 38 cm in the sediment (Carignan 1985). The contradicting trends observed in porewater SRP at lakes Narrow, Wingra, and Memphremagog may be caused by differences in macrophytes and sediment characteristics. The aquatic macrophyte at Narrow Lake was *Vallisneria* sp.; in lakes Wingra and Memphremagog it was *Myriophyllum spicatum*. Exchangeable P and porewater pH may differ in the three lakes. Because exchangeable P in particulate sediments may buffer porewater [SRP] and porewater [SRP] depend partly on pH (Ku et al. 1978; Carignan 1985), differences in exchangeable P and porewater pH may explain the different trends of porewater SRP over the summer.

Trends of porewater [SRP] over the summer also differed between sites colonized by macrophytes and those without macrophytes. At Narrow Lake, porewater [SRP] decreased from late June to August in a site colonized by macrophytes and varied inconsistently in a site without macrophytes. These trends are similar to those observed in Lake Memphremagog (Carignan 1985), where areas cleared of macrophytes were compared with noncleared sites. Uptake of P by macrophyte roots during the macrophyte growing season may explain different patterns in porewater SRP concentrations over the summer at sites with and without macrophytes (Carignan 1985). At Narrow Lake, porewater [SRP] in the shallow site with macrophytes were higher than in the site without macrophytes. The presence of macrophytes may increase P deposition and decrease mixing of porewater with lakewater. Increased mineralization of sedimented material and decreased mixing between porewater and lakewater could increase porewater [SRP] (Carignan 1984a).

At two depths in Narrow Lake not colonized by macrophytes, no trends in porewater [SRP] from late June to August were observed (Fig. 4). These patterns were somewhat different from those observed at two sites, not colonized by macrophytes, in Lake Mendota (Holdren et al. 1977). At Lake Mendota, porewater [SRP] increased over the summer at the shallow site, whereas they did not change at the deep site. Trends in porewater [SRP] over the summer may differ at the two lakes due to sediment P release. Mixing, pH, redox potential, and particulate sediments influence P release from sediments (Bostrom et al. 1982); these processes may be different at the two lakes.

At Narrow Lake, variance of [SRP] over the entire porewater profile was not significantly different between a small site (<0.15 m^2) and the entire lake. Although, average porewater [SRP] were higher over the entire lake than within the small site, differences between [SRP] in the top 5 cm of the sediment

were not significant (t-test; $P>0.2$). Porewater [SRP] in another lake varied one order of magnitude in three sites far apart but at similar depth (Drake and Heany 1987). Carignan (1985) also found substantial variation in porewater [SRP] from four peepers within one site.

A strong relationship between porewater [SRP] and depth at Narrow Lake was evident when data from macrophyte sites were excluded (Fig. 5). Relationships between porewater [SRP] and depth were similar during 1985, and in 1985 and 1986 (ANCOVA; residual variance $P>0.25$, slope $P>0.5$, intercept $P>0.5$). Differences in the relationship between porewater [SRP] and depth in three transects, sampled in 1985, were tested. Although the three transects were far apart, the relationship between lake depth and porewater [SRP] (in the top 5 cm of the sediment) were very similar (ANCOVA; residual variances, slopes, and elevations: $P>0.5$). Presence of macrophytes can obscure trends with depth (Holdren et al. 1977; Carignan 1984a). To our knowledge, the consistent increase of porewater [SRP] with lake depth at Narrow Lake is the first significant relationship reported in the literature, although other data are consistent with this trend (Bannerman et al. 1974; Holdren et al. 1977; Carignan 1984a; Psenner and Pucsko 1988).

During summer, release of SRP from shallow sediments in Narrow Lake averaged 0.11 $mg \cdot m^{-2} \cdot d^{-1}$. The contribution of P from the sediments in the trophogenic zone (46.8% of lake surface area) to the entire lake was 0.05 $mg \cdot m^{-2} \cdot d^{-1}$. The contribution of SRP from sediments to overlying water is underestimated by this calculation since the gradients are (1) likely much steeper just below the sediment–water interface, and (2) release is enhanced in shallow sediments by bioturbation, mixing, and groundwater flow. Even so, our conservative estimate of P release rate from shallow sediments is 29% of the P input by atmospheric deposition from May to August (0.18 $mg \cdot m^{-2} \cdot d^{-1}$, Shaw et al. 1989). Narrow Lake has a small drainage basin (7 km^2) and beaver dams limit runoff from its watershed (the lake level is consistently lower than the water level at the other side of the dams). Thus, atmospheric deposition is the major external input of P to the lake. SRP release from shallow sediments into lakewater represents at least one-fourth of the major external source of P to Narrow Lake.

To calculate P release from shallow sediments directly into the epilimnion, a sampling design to monitor porewater P should focus on sediments in the trophogenic zone with and without macrophytes. At Narrow Lake, average [SRP] in the top 5 cm of the sediment and variance at the 5-m depth were not statistically different between either a small site and the entire lake, or four depths in three transects. However, porewater [SRP] increased substantially with lake depth. Sampling effort could thus be limited to one transect. Based on the Narrow Lake data, the required number of peepers for the top 5 cm in the sediment at one site was seven (calculated from the small site data Table 1, with a desired ratio of SE to mean of 50% and a 90% confidence interval). Since [SRP] increased with lake depth, porewater should be collected at three or more depths in a transect. At a deep site, sampling may be restricted to one date during the summer. However, samples should be collected at least monthly from shallow sites because temperature and macrophytes may influence porewater [SRP].

Summer and spatial trends of porewater SRP at Narrow Lake were used to derive a strategy to sample porewater efficiently. At Narrow Lake, calculation of a P release rate was feasible; this release was important relative to the major external P source. More information is needed on a range of lake types to determine the generality of the seasonal and spatial trends in porewater SRP observed at Narrow Lake and the impact of P release from shallow sediments into aerobic lakewater at other lakes.

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Quantitative and Qualitative Characteristics of Somatic and Gonadal Growth of Yellow Perch (*Perca flavescens*) from Lac Ste. Anne, Alberta

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A yellow perch (*Perca flavescens*) population from a shallow eutrophic north temperate lake was sampled 10 times between March 1976 and June 1977 to determine the characteristics of somatic and gonadal growth. Quantitatively, somatic growth differed in timing and extent among age–sex groups. One+ males and females grew mostly in June whereas 2+ males grew mainly in July; 2+ females grew from June through September. Two+ males grew less over the year than did the other age–sex groups. The qualitative characteristics of somatic growth were not influenced by sex or maturation. The timing of gonadal growth and the associated endogenous energy utilization differed between the sexes. One+ females did not mature. Testes grew in late summer (August). There was no impact of gonad development on somatic composition of 1+ males whereas 2+ males appeared to use visceral fat. Gonadal growth for 2+ females began in August and continued through March and presumably to spawning in April; somatic lipid was depleted during ovarian growth.

Une population de perchaude d'un lac eutrophe peu profond, tempéré nord a été échantillonné 10 fois entre mars 1976 et juin 1977 afin de déterminer les caractéristiques de la croissance somatique et de la croissance gonadique. Sur le plan quantitatif, la croissance somatique différait au niveau du moment et de son étendue entre les groupes d'âge et selon le sexe. Les mâles et les femelles d'âge 1+ croissaient en grande partie en juin tandis que la croissance des mâles d'âge 2+ avait lieu surtout en juillet; la croissance des femelles d'âge 2+ s'effectuait de juin à septembre. Les mâles d'âge 2+ se développaient moins au cours de l'année que les autres groupes d'âge et selon le sexe. Les caractéristiques qualitatives de la croissance somatique n'étaient pas influencées par le sexe ou la maturation. Le moment de la croissance gonadique et l'utilisation associée de l'énergie endogène différaient entre les sexes. Une femelle d'âge 1+ n'atteignait pas la maturité. Les testicules se développaient à la fin de l'été (août). Le développement des gonades n'avait pas de répercussion sur la composition somatique des mâles d'âge 1+ tandis que des mâles d'âge 2+ semblaient utiliser la graisse viscérale. La croissance gonadique chez les femelles d'âge 2+ commençait en août et se poursuivait jusqu'en mars et probablement jusqu'à la fraye en avril; il y avait épuisement des lipides somatiques pendant la période de développement des ovaires.

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The composition of a fish's body changes continuously during the year. Water, protein, lipid, and ash are accumulated during somatic growth and lipid and/or protein can be depleted during gonadal growth.

Although a large amount of information exists on the quantitative characteristics of body growth in yellow perch (*Perca flavescens*) (e.g. Hile and Jobes 1940; Pycha and Smith 1955; Grimaldi and Leduc 1973), there is no information on the qualitative aspects of somatic growth, i.e. the roles played by water, protein, fat, and ash in increases in somatic weight. Weatherley and Gill (1987) reviewed experimental studies which examined changes in body composition with growth; however, these investigations were restricted to short-term studies of immature fish held at various temperatures and fed at specific ration levels. Only Shul'man (1974) has discussed the qualitative characteristics of fish growth with respect to wild populations over growth seasons. Craig (1977) has described the seasonal cycles of somatic composition of European perch (*Perca fluviatilis*) from which qualitative somatic growth can be inferred. However, he worked with sexually mature fish only and expressed his data in terms of a fish of standard length. Consequently, the influence of sexual maturity and body size on the qualitative characteristics of somatic growth could not be determined.

As for somatic growth, only the quantitative aspects of gonadal growth of yellow perch has been investigated. Thorpe (1977) has summarized information on the quantitative characteristics of gonadal growth of European and yellow perch. Testes growth occurs in August whereas ovarian growth begins in July and continues steadily until spawning, usually in April. Craig (1977) has examined the qualitative characteristics of gonad growth in European perch. He found that testes growth occurred in August as a result of protein and water accumula-

tion; lipid weight was proportional to testes weight through the year. Ovarian growth took place as a result of a continuous accumulation of water, protein, and lipid with protein content appearing to increase at a higher rate.

No study has determined the role that the soma plays in gonadal growth of yellow perch. Newsome and Leduc (1975) found that most of the total fat content of mature female yellow perch was concentrated in the ovary at least 4 mo before spawning. Makarova (1973) and Craig (1977) examined the involvement of somatic constituents in gonadal growth of European perch. Makarova (1973) studied seasonal changes in visceral fat content and liver weight. He concluded that testicular growth occurred at the expense of liver lipid and mesenteric fat, and suggested that ovarian development used endogenous protein and exogenous lipid. Craig (1977) found that testes growth of European perch from Lake Windermere was initially associated with a depletion of somatic fat followed by depletion of somatic protein whereas ovarian growth was associated with a continuous depletion of somatic protein and lipid. Neither study considered the effect of body size on the use of somatic constituents for gonadal growth.

The purpose of our study was to determine the quantitative and qualitative characteristics of somatic and gonadal growth of yellow perch from Lac Ste. Anne, Alberta and to examine the influence of gonadal growth on somatic composition. We hoped to answer several questions regarding somatic and gonadal growth: (1) do sex, maturity, and age (size) affect the timing and extent of growth, (2) do these factors influence how the fish accumulates mass, i.e. do protein, lipid, and water play the same roles in the increase in body weight, and (3) how are somatic constituents involved with gonadal growth and could this be influenced by sex and age?

Materials and Methods

Lac Ste. Anne (114°24′W, 53°43′N) is a large (surface area 57 km^2), shallow (average depth 4.8 m), eutrophic lake located 75 km west-northwest of Edmonton, Alberta. The water is usually isothermal during the summer (14–18°C from May to October) and winter (1–3°C from November to April). Only during brief periods in October and April do water temperatures differ substantially from one of these two regimes (Diana and Mackay 1979).

Yellow perch were collected on 10 occasions between March 1976 and June 1977. In summer, they were collected using gillnets, a 5-m, semi-balloon, otter trawl and a beachseine, and in winter using gillnets. Upon capture, the fish were taken to the Lac Ste. Anne Biological Station where the sample was divided on the basis of sex and apparent age. Sex was determined visually through an incision made in the ventral mid-line. Age was inferred from standard length. When sample size permitted, 25 individuals of each sex were selected at random from each age group. For each fish, the left opercular bone was removed to confirm age using the method described by Bardach (1955). Somatic wet weight was measured to the nearest 0.01 g after removing the gonad, emptying the stomach and intestinal contents, and blotting the body dry. The soma was then placed in a numbered plastic bag and stored at −30°C. The gonads were blotted dry, weighed to 0.001 g, and then stored in a numbered, sealed vial at −30°C. GSI, the gonosomatic index, was estimated as the percentage of the total body weight ascribed to gonad weight.

The soma of a maximum of 10 fish from each age–sex group were selected at random for proximate analysis. Additional bodies were selected when larger sample sizes were needed for protein or lipid analysis. Each was dried to constant weight at 70°C and reweighed to 0.01 g to estimate water content. The soma was then ground into a fine powder using an electric household coffee grinder. This powder was stored in a sealed vial at −30°C for protein and lipid determinations.

Initially somatic lipid and protein contents (percent dry somatic weight) were determined for five individuals from each group. The sample size (n) which would provide a 95% fiducial limit interval which was 6% of the mean was calculated using the equation:

$$n = 4(s)^2/L^2,$$

where s and L are the standard deviation and 3% of the mean of the five determinations, respectively (Snedecor and Cochran 1967). Analyses were conducted until samples from 10 individuals were analysed or the number of determinations made exceeded the calculated sample size required. A precision of 3% of the mean value was selected because this gave the best estimate of the mean without a large increase in the number of fish which had to be analysed.

Somatic protein content was determined using a semi-micro modification of the Kjeldahl method (Steyermark 1961). THAM (Tris-(hydroxymethyl)-aminomethane, Fisher certified primary standard) was used as a standard. It contained 11.06 ± 0.41% (mean ± SD) nitrogen over all sessions of nitrogen determination. This was not significantly different ($t = 1.44$, $0.05 < p < 0.10$) from THAM's theoretical nitrogen content (11.65%). Blanks were run with each series of samples to correct for nitrogen contamination of reagents. Total protein nitrogen (TPN) was calculated from total nitrogen (TN) using the correction described by Craig (1977) where:

$$\text{TPN} = \text{TN} - (\text{TN} \times \text{C})$$

and C, the nonprotein nitrogen, was 0.1580 of total nitrogen. TPN was multiplied by 6.25 to give somatic protein.

Somatic lipid and visceral fat contents (percent visceral fat dry somatic weight) were determined gravimetrically using the procedure described by Medford and Mackay (1978). Lipid was extracted by refluxing powdered fish or dried viscera in a Soxhlet apparatus for 4.5 to 5 h with a 2:1 mixture of chloroform and methanol. For determinations of visceral fat content, lipid was extracted from viscera dried to constant weight at 70°C. The viscera were taken from fish which had not been ground up for proximate analysis. Blanks were run with each set of samples to correct for error due to nonvolatile contaminants of the choloroform/methanol mixture. A pool of ground perch somatic powder was used as a standard to detect any differences between sets of analyses. The standard contained 7.26 ± 0.28% (mean ± SD) lipid. A powdered sample of pike (*Esox lucius*) ovary was used as a standard for visceral fat determinations because its lipid content was similar to that of perch viscera. The pike ovary contained 15.72 ± 0.69% (mean ± SD) lipid.

Ash and carbohydrate contents of the soma were not determined. They were assumed to be 6.2 and less than 1% dry somatic weight, respectively (Craig 1977).

Lipid, protein, and water contents of gonads were determined for maturing fish collected between September and March. The gonads analysed were from fish used for proximate analysis. Gonads were dried at 70°C to a constant weight; dry

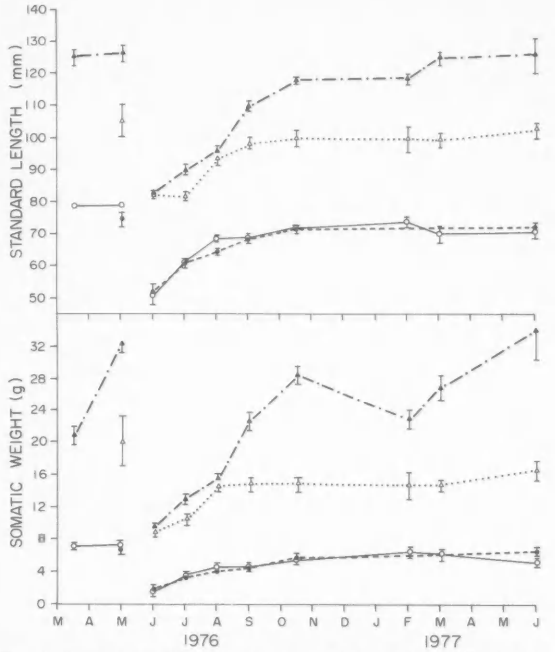

FIG. 1. Somatic weight (grams) and standard length (millimetres) of yellow perch from Lac Ste. Anne. March 1976–June 1977. $\bar{x} \pm S\bar{x}$. Standard errors are not shown when they are narrower than the symbols used to locate the mean value. One+ male (○, —), 1+ female (●, ——), 2+ male (Δ, ●●●), 2+ female (▲,-●-).

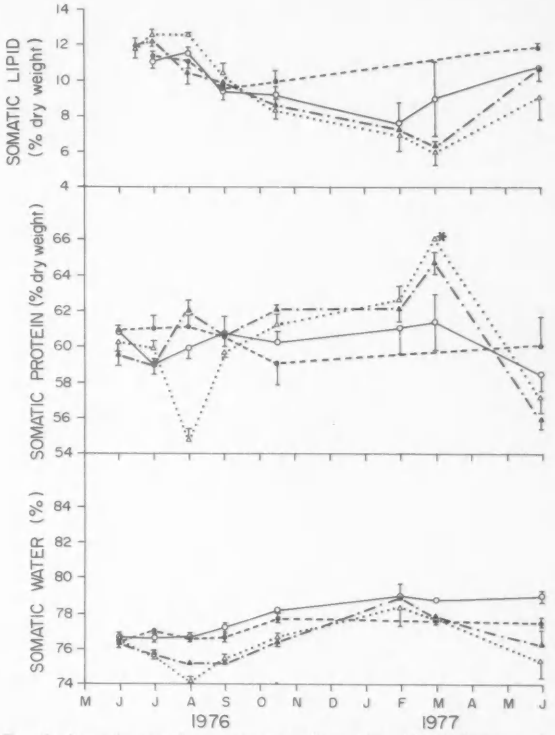

FIG. 2. Somatic constituent concentrations. Asterisks indicate $n = 1$. Symbols as in Fig. 1.

gonad weight was then measured to the nearest 0.001 g. The gonads were individually ground to a powder using a mortar and pestle. The powder was returned to the appropriate vial and stored at −30°C for proximate analysis.

Lipid content (perent dry gonad weight) was determined spectrophotometrically using a modification of the method for total serum lipid determination of Frings et al. (1972) (Tanasichuk 1978). Finely ground pike ovary was used as a standard. It contained 16.65 ± 0.41% (mean ± SD) lipid as determined gravimetrically using the procedure described by Medford and Mackay (1978) and 16.21 ± 1.59% (mean ± SD) lipid as determined using the modified technique of Frings et al. (1972). These two values were not significantly different ($t = 1.10$, $0.20 < p < 0.40$).

Gonad protein content (percent dry gonad weight) was determined using the micro-Kjeldahl method described by Steyermark (1961). THAM was used as a standard; it contained 10.82 ± 1.02% (mean ± SD) nitrogen. This was not significantly different ($t = 0.61$, $0.50 < p < 0.9$) from the theoretical value of 11.65%. Gonad protein content was estimated using the calculations described for somatic protein. Mean percentage values, on a dry weight basis, for nonprotein nitrogen in testis and ovary were assumed to be 1.62 and 0.95%, respectively (Craig 1977).

Ash and carbohydrate contents of the gonad were not determined. We assumed that they were 5.2 and 1.4% dry weight, and 10.2 and 2.4% dry weight, for testes and ovaries, respectively (Craig 1977).

One-way analyses of variance were used to test for significant differences in mean size, gonad weight and water, protein and lipid concentrations between sampling periods, and age–sex groups. Percentage data, excluding those for somatic protein, were transformed with the arc sine transformation (Sokal and Rohlf 1981) before analysis. Differences were tested using the Dunn–Sidak method (Sokal and Rohlf 1981) and were considered significant if $p < 0.05$.

Results pertain to 1+ and 2+ perch because older fish and young-of-the-year could not be collected routinely.

Results

Somatic Growth

The extent of somatic growth of 1+ males and females was similar although its timing differed (Fig. 1). There were no significant differences in mean standard length between sexes at any sampling period even though length increased significantly in June and July for males and in June and September for females. Trends in somatic weight growth were similar to those for length. Approximately half the year's growth occurred in June.

In contrast with 1+ perch, 2+ males and females showed very different trends in somatic growth (Fig. 1). For males, length increased significantly in July. Weight did not increase significantly between any consecutive sampling periods but increased significantly between June and August. Females grew significantly in length in August. Although weight did not increase significantly between consecutive months, it was significantly greater in September than in June (Fig. 1). By June 1977 2+ females were 105% heavier than 2+ males. Females were significantly heavier than males at all sampling dates and

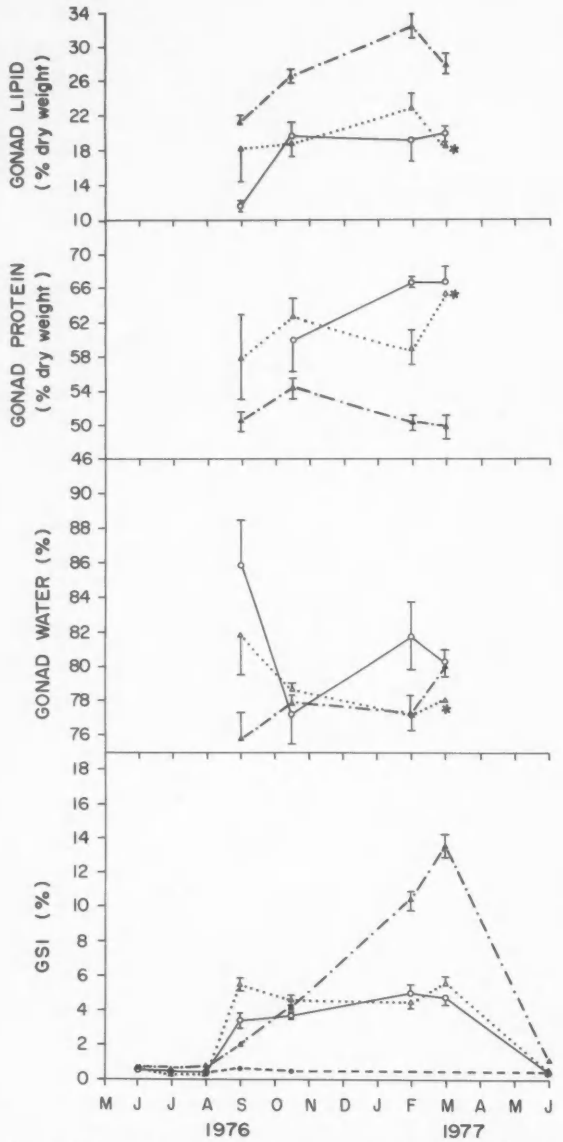

FIG. 3. GSI and gonadal constituent concentrations. Symbols as in Fig. 1.

longer except in June and August; the insignificant difference in August appears to result from most somatic growth of males occurring in July.

Length and weight at capture of fish collected as 1+ in May 1976 and 2+ in June 1976 did not differ significantly. Therefore growth of yellow perch from Lac Ste. Anne appeared to begin in June.

The annual growth increment varied among age–sex groups. Increases in length and weight over the year (between June 1976 and June 1977) were similar between 1+ males and females (males, 42% in length and 231% in weight; females, 38% in length and 231% in weight). Two+ males increased the least in both length (24%) and weight (89%). The length and weight of 2+ females increased by 51 and 270%, respectively.

Proximate analysis accurately described the somatic composition of all age–sex groups. The sums of water, protein, lipid, and ash estimates accounted for 94.7 ± 0.65 (mean $\pm$ SD) percent of the mean somatic weights for all age–sex groups. Protein and lipid were expressed on a dry weight basis to uncouple the influence of changes in water content from fluctuations in these nonaqueous constituents.

There were minor differences in qualitative growth between sexes for 1+ fish (Fig. 2). Somatic growth of 1+ males occurred with no significant changes in the concentration of any constituent. This occurred for 1+ females in June; however, growth in September took place with a preferential accumulation of water. Protein and lipid composition of 1+ males and females did not differ significantly within sampling periods throughout the year.

The qualitative characteristics of somatic growth of 2+ males were more complicated than for the other age–sex groups (Fig. 2). Somatic growth took place with no significant changes in water or lipid concentrations. However, protein concentration declined significantly in July indicating that it was being accumulated more slowly than somatic weight was increasing (protein weight did not decline significantly in July). Lipid declined significantly between August and October.

Somatic growth of 2+ females took place with insignificant changes in the concentrations of somatic constituents (Fig. 2). As in 2+ males, protein concentration declined in late winter.

Somatic composition was remarkably similar among age–sex groups over the June 1976–77 growth year. Lipid concentrations were not significantly different between groups at any sampling period. Protein concentrations were different in August only because they were significantly lower in 2+ males. Although water concentrations did differ somewhat, the qualitative characteristics of energy (i.e. protein and lipid) accumulation did not appear to be influenced by age (size), sex, or maturation.

Gonadal Growth

The quantitative characteristics of gonadal growth differed between sexes (Fig. 3). GSI increased significantly in August for males. GSI of 1+ females did not change significantly over the year; however, the GSI of 2+ females began increasing in August and increased significantly from October through March.

Proximate analysis accounted for an average of $97.7 \pm 0.90\%$ (mean $\pm$ SD) of gonadal weight. Testes composition was similar between age groups at most sampling periods. The only exception was that the protein concentration of the 1+ male gonad was significantly greater in January. Testes composition for 2+ males did not change between September and March. Ovarian growth occurred with no significant changes in protein and water concentrations and a preferential accumulation of lipid in September.

There is a suggestion that larger male yellow perch from Lac Ste. Anne use visceral fat reserves for gonad development, although the results of *t*-test indicate that visceral fat contents did not differ significantly ($0.10 > p > 0.05$) between months for each sex and between sexes for a given month (Table 1).

Discussion

Our results indicate that the qualitative characteristics of somatic growth of yellow perch are not influenced by age (size),

TABLE 1. Somatic and visceral fat contents (grams dry weight) of 2+ perch. $\bar{x} \pm S_{\bar{x}}$

	1976				1977
	June 2–3	July 6–7	Aug. 3–4	Sept. 7–8	Mar. 2–3
			2+ males		
Somatic lipid	0.24 ± 0.010	0.3 ± 0.01	0.5 ± 0.01	0.4 ± 0.02	0.20 ± 0.020
n	13	10	4	8	4
Visceral fat	0.03 ± 0.007	0.016 ± 0.0020	0.13 ± 0.067	0.04 ± 0.005	0.04 ± 0.006
n	5	3	5	5	5
Somatic–visceral	0.21	0.31	0.37	0.36	0.16
			2+ females		
Somatic lipid	0.26 ± 0.010	0.4 ± 0.01	0.4 ± 0.02	0.6 ± 0.02	0.4 ± 0.02
n	13	10	9	10	9
Visceral fat	0.04 ± 0.004	0.028 ± 0.0050	0.08 ± 0.025	0.07 ± 0.012	0.05 ± 0.005
n	5	5	5	5	5
Somatic–visceral	0.22	0.37	0.32	0.53	0.35

sex, or maturity; there was no preferential accumulation of lipid and/or protein among age–sex groups. Consequently, it appears that the qualitative characteristics of energy accumulation were not influenced by these factors, i.e. immature (1+) perch showed the same trends in protein and lipid acquisition as did the other age–sex groups; the only exception was the decline of protein in 2+ males during July. Because 1+ females were not collected over winter, we could not compare variations in somatic composition between immature and mature fish then. There is a decline in lipid in males and 2+ females during winter which seems to reflect starvation in males and likely starvation and ovarian growth in females. The late-winter depletion of protein in 2+ fish may reflect a size-dependent energy drain similar to the prespawning starvation observed in northern pike (Diana and Mackay 1979). Our results for yellow perch support those of Eliassen and Vahl (1982) for cod (*Gadus morhua*), i.e. variations in tissue energy content were similar between immature and mature fish.

Our results differed from those inferred from Craig (1977) who described seasonal changes in somatic composition of European perch from Lake Windermere. He reported that there were significant differences between monthly regression equations for somatic weight against water, fat, and protein for males but no significant differences for females; this implies that changes in protein, lipid, and water concentations were disproportional to somatic weight changes in males. However, we examined growth in fish much smaller than Craig (1977) did and differences in the results could be due to the effect of fish size, possibly in the context of an influence of size on the energy demand for gonad development. In addition, Craig described protein and lipid contents on a wet weight basis which could have resulted in them being confounded by changes in water content.

The quantitative characteristics of somatic growth of 1+ and 2+ yellow perch from Lac Ste. Anne seem typical for the species (e.g. Langford and Martin 1940; Jobes 1952; Pycha and Smith 1955; Ney and Smith 1975). In general, yellow perch from Lac Ste. Anne grew during summer (June–September). Lengths and weights at age were similar to those for perch from Lake Huron (Hile and Jobes 1940), Quebec (Grimaldi and Leduc 1973), and Minnesota (Ney and Smith 1975). Yellow perch from Lac Ste. Anne also exhibit growth characteristics similar to those which LeCren (1958) has described for perch from Windermere, i.e. the tendency for adult females to grow faster than adult males.

We hypothesize that the sex-specific differences in growth rate of mature fish reflects a strategy that females employ to maximize their reproductive effort. Wootton (1979) suggested that investment of energy into growth rather than egg production would subsequently be reflected in a greater fecundity. Sheri and Power (1969) developed an equation from which fecundity (Y) can be predicted from fork length (X), where

$$\log_{10} Y = 2.982 + 0.007(X)$$

and $r = 0.85$. Using this equation and the factor Carlander (1950) provides for converting standard length to fork length (fork length = 1.102 × standard length), we calculated fecundity for yellow perch at the mean standard lengths of 2+ males and females in October, when females stopped growing in length. We estimated that the higher growth rate of the females would result in a 38% (from 5627 to 7789 eggs) increase in fecundity, assuming no change in egg size.

The sexual dimorphism in growth of mature yellow perch may have resulted from the influence of sex steroids. Peter (1979) suggested that the sexual dimorphism regarding size-at-age in fish may be due to the effect of sex steroids on food intake. Yellow perch from Lac Ste. Anne showed no differences in size-at-age until the females entered the year of life when they became sexually mature.

The quantitative characteristics of gonadal growth for yellow perch from Lac Ste. Anne are similar to those presented by Thorpe (1977) for European and yellow perch and by Craig for European perch; however, the qualitative characteristics differ from those Craig described. GSI for males in March (~5%) is similar to that described by LeCren (1951) and Turner (1919) for European and yellow perch. Female GSI in March was 13.5%, somewhat lower than that reported by LeCren (1951) for European perch. We suspect that the GSI's of yellow perch collected nearer to spawning (April–May) would have been higher. The differences in qualitative characteristics of gonad growth appear to be due to our analyses being limited to Sep-

tember–March and Craig describing his protein and lipid contents on a percent wet weight basis.

One+ males appeared to use no endogenous energy sources for testes growth whereas 2+ fish seemed to use lipid. These results supported those of Newsome and Leduc (1975) but were contrary to those of Makarova (1973) and Craig (1977). These authors reported that protein is utilized for ovary and testes development. This difference could be due to these workers dealing with larger fish which would require more energy for gonad growth.

Depletion of visceral fat reserves during the early stages of gonadal recrudescence similar to that suggested for yellow perch (Table 1) occurs in Atlantic herring (Gakichko and Dubrovskaya 1970), lake whitefish (Reshetnikov et al. 1970), Arctic char (Matsuk and Lapin 1972), and European perch (Makarova 1973). The behaviour of visceral fat deposits of perch from Lac Ste. Anne is similar to that described by Makarova (1973) for European perch. In both populations, visceral fat deposits were built up in summer. Males had twice the visceral fat of females in August and the overall rise and fall of visceral fat was more dramatic in males. For male yellow perch from Lac Ste. Anne, changes in visceral fat content accounted for virtually all the variation in somatic lipid during July and August when somatic and gonadal growth were most intensive. Krivobok and Shatunovskiy (1971) suggested that the more intensive accumulation and reduction of visceral fat, which is observed in male perch, is associated with greater activity of lipid metabolism, especially phospholipid metabolism, in the course of spermatogenesis. Based on Turner's (1919) description of the maturation processes of male yellow perch, August would be the period of spermatogonia proliferation and the beginning of spermatogenesis for yellow perch in Lac Ste. Anne.

Acknolewdgments

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Prey Detection in Cyprinids during Early Development[1]

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Wanzenböck, J., and F. Schiemer. 1989. Prey detection in cyprinids during early development. Can. J. Fish. Aquat. Sci. 46: 46: 995–1001.

Larval and juvenile fish of roach (*Rutilus rutilus* L.), bleak (*Alburnus alburnus* L.), and blue bream (*Abramis ballerus* L.) were investigated weekly to define the ontogenetic development of prey detection capacities. Visual acuity was determined by measuring reactive distances for zooplankton prey for fish from 8 to 50 mm standard length using video recordings. Data of reactive distances, swimming speeds, and the characteristics of the visual field were combined to calculate prey location volumes. Prey location capacity increased exponentially with fish size which implies enormous differences in prey encounter rates among size classes of cyprinids. Distinct differences of prey location capacities occurred between species in the juvenile, planktivorous stages of the three cyprinids coinciding with the trophic differentiation of the adults.

Dans le but de définir le développement ontogénétique de l'aptitude à déceler des proies, des larves et des juvéniles de *Rutilus rutilus* L., d'*Alburnus alburnus* L. et d'*Abramis ballerus* L. ont fait l'objet d'études hebdomadaires. L'acuité visuelle a été établie en mesurant au moyen d'enregistrements vidéo les distances de réaction à la présence des proies zooplanctoniques dans le cas de poisson dont la longueur standard était comprise entre 8 et 50 mm. Les données relatives aux distances de réaction, à la vitesse de nage et les caractéristiques du champ visuel ont été combinées afin de calculer le lieu d'occupation des proies en trois dimensions. La capacité de l'endroit où se trouve les proies augmentait de façon exponentielle avec la taille du poisson ce qui signifie des différences importantes au niveau du taux de rencontre des proies au sein des classes de taille des cyprinidés. Il existait des différences marquées au niveau de la capacité de l'emplacement des proies entre les espèces au niveau des stades planctivores, juvéniles des trois cyprinidés étudiés ce qui coïncide avec la différentiation trophique des adultes.

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Planktivorous fish are a major factor influencing the species and size composition of zooplankton in freshwater ecosystems (Hrbáček et al. 1961; Brooks and Dodson 1965; see reviews by Lazzaro 1987; and Northcote 1988). In analyzing this phenomenon many authors have developed predictive models for prey selection in fish (Ware 1973; Werner and Hall 1974; O'Brien et al. 1976; Wright and O'Brien 1984). A significant component of these models is the reactive distance (RD) of the predator, i.e. the distance at which the fish responds to a particular prey item.

Early studies established that RD is a function of prey size (Werner and Hall 1974; O'Brien et al. 1976; Confer et al. 1978). Other factors found to influence RD are visibility and conspicuousness of prey (Zaret and Kerfoot 1975) as well as light and

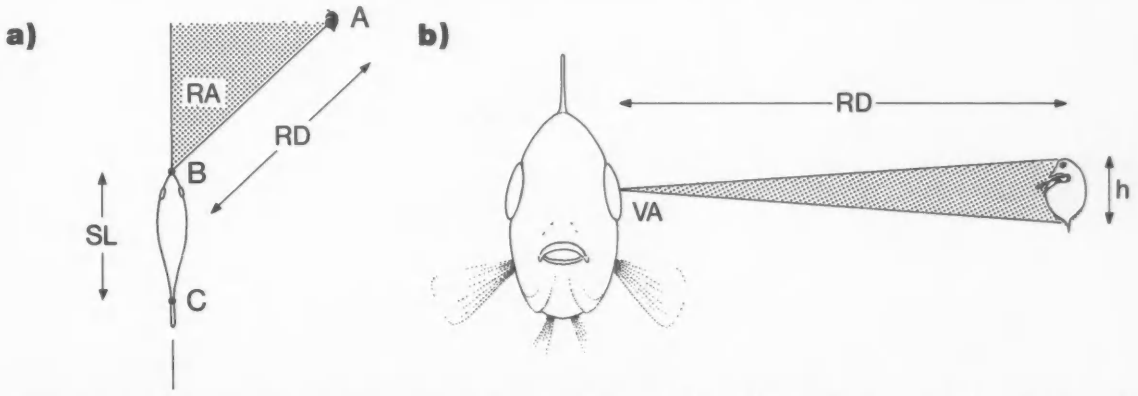

FIG. 1. (a) Analysis of video records. A = position of prey; B = snout of the fish; C = bases of caudal fin; SL = standard length; RD = reactive distance; RA = reaction angle. (b) The visual angle (VA) computed from RD and body length of prey (*h*).

[1]Dedicated to Professor Dr. Wolfgang Wieser on the occasion of his 65th birthday.

TABLE 1. Dimensions of experimental tanks, water volumes, and water depth used with different sized fish.

Fish (all three species)		Experimental tanks		
Age (d)	Standard length (mm)	Diameter (cm)	Volume (mL)	Water depth (cm)
12–26	7–13	15	150	0.85
26–40	13–18	20	300	0.95
40–48	18–20	25	1000	2.04
48–60	20–25	25	2000	4.08
60–90	25–50	30	3000	4.24

turbidity (Confer and Blades 1975; Vinyard and O'Brien 1976). Recently Breck and Gitter (1983); Dunbrack and Dill (1983); Hairston et al. (1982); and Li et al. (1985) found that RD increases with fish size during ontogenetic development. However, only a few detailed studies on the ontogenetic development of prey detection characteristics after the onset of exogenous feeding have been carried out (Braum 1964; Rosenthal and Hempel 1970; Blaxter and Staines 1971; Hunter 1972; Hoagman 1974; available data are summarized in Blaxter 1986). Many fish species are zooplanktivorous during this phase but exhibit a distinct differentiation in their foraging biology during later development. It can be assumed that this shift in feeding modes is related to different optical requirements. Thus the question arises to which extent the different optical requirements, e.g. the RDs, of foraging in the adults are already expressed in the larval and juvenile phase.

Extensive literature exists on the reactive distances of sunfish (Luecke and O'Brien 1981; Breck and Gitter 1983; O'Brien et al. 1986) and salmonids (Confer et al. 1978; Dunbrack and Dill 1984). Comparable data for cyprinids are lacking. In Europe, cyprinids are the dominant fish family in terms of species number and often occur in high abundances. They show a remarkable diversity of ecological differentiation in the adult phase.

The major goal of this study was to investigate the ontogenetic development of prey recognition capacities (measured as RD) of three European cyprinid species during the first 3 mo after hatching. The comparative approach was chosen (a) to define possible interspecific differences in this early phase of development and (b) to answer the question to which extent these differences reflect the trophical differentiation of the adults. Three species with different feeding biologies in the adult stage were chosen for comparison. The roach (*Rutilus rutilus* L.) can be characterized as an omnivorous fish with a wide food spectrum including detritus, plant material, zoobenthos, and zooplankton (Prejs 1976). Zooplanktivorous feeding has been observed only in water bodies with high zooplankton abundance (Bohl 1980; Persson 1983a,b; Brabrand 1985; Filka et al. (unpubl. data)). The bleak (*Alburnus alburnus* L.) is a more optically oriented fish (Kotrschal and Junger 1988) specialized in surface and zooplankton feeding (Prejs 1976; Filka et al. (unpubl. data)). The blue bream (*Abramis ballerus* L.) is a zooplankton specialist (Lelek 1987). The characteristics of the feeding biology of these species is well correlated with their morphology, e.g. with the oropharyngeal system (Polha et al. 1986) and of the sensory centers of the brain (Kotrschal and Junger 1988). In the larval and juvenile stages all three species are optically oriented particle feeders with a high preference for zooplankton (Panova 1966; Cryer et al. 1986; Mark et al. 1987; Keckeis et al. 1988).

Materials and Methods

Adults of roach, bleak, and blue bream were caught in a backwater of the river Danube near Vienna (Austria) by gill-

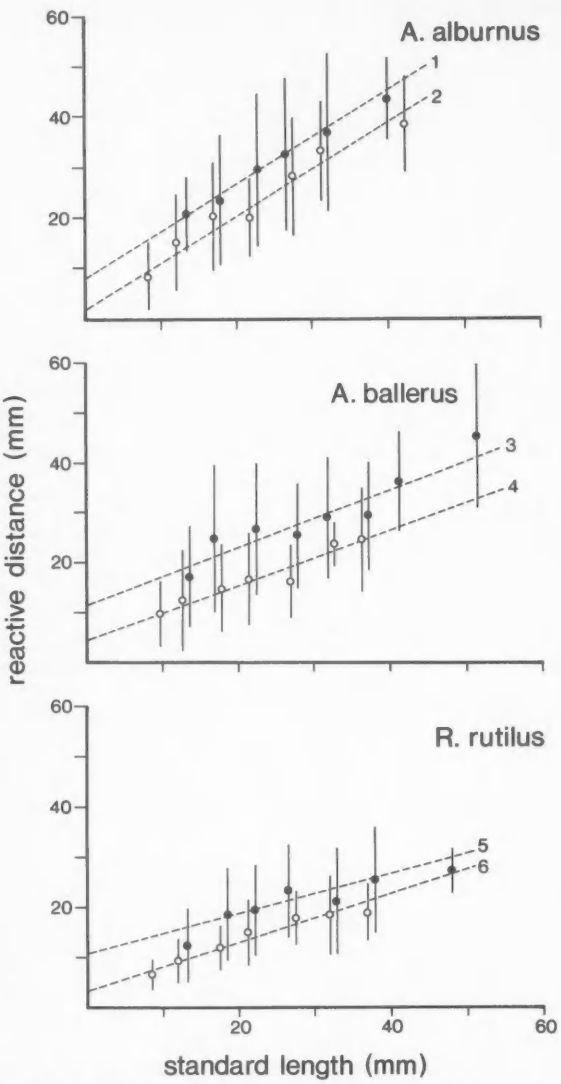

FIG. 2. Reactive distances versus standard length of fish for two size classes of *Ceriodaphnia reticulata* (full circles: 0.65 mm, open circles: 0.49 mm). Symbols represent mean RDs of each size category of fish, vertical bars indicate ±1SD.
Regression equations:
A. alburnus: (1) RD = 7.38 + 0.91 · SL, $r = 0.38$, $n = 206$
(2) RD = 1.82 + 0.91 · SL, $r = 0.58$, $n = 266$
A. ballerus: (3) RD = 11.36 + 0.57 · SL, $r = 0.38$, $n = 230$
(4) RD = 4.59 + 0.52 · SL, $r = 0.35$, $n = 301$
R. rutilus: (5) RD = 10.62 + 0.37 · SL, $r = 0.28$, $n = 196$.
(6) RD = 3.05 + 0.47 · SL, $r = 0.61$, $n = 327$

netting. Artificial fertilization of eggs and rearing of young fish was carried out according to standard aquacultural techniques (Tölg 1981). Fish stocks were kept in circular pools (60 L) with constant water flow at 20°C and a 16-h light period. They were fed ad libitum with *Artemia salina* nauplii and natural zooplankton.

Prey for the experiments was obtained from laboratory cultures. Two distinct size classes of *Ceriodaphnia reticulata*

TABLE 2. Analysis of covariance of regressions relating RD to standard length. Regression numbers refer to Fig. 2. Pairs tested: 1–2, 3–4, 5–6 (intraspecific, small versus large prey); 1–3, 1–5, 3–5 (interspecific, large prey); 2–4, 2–6, 4–6 (interspecific, small prey). Intercepts are compared for those pairs in which slopes are not significantly different. Values above the diagonal refer to slopes, below the diagonal to intercepts. Values marked **: significant on the 0.05 level, values marked *: significant on the 0.1 level, ns = not significant on the 0.05 level.

Regression		*A. alburnus*		*A. ballerus*		*R. rutilus*	
No. test for		1	2	3	4	5	6
linearity	(F)	0.17**	2.29*	1.5**	0.89**	1.13**	1.83**
Regression No.							
A. alburnus	1		0.007 ns	2.35**		3.51**	
	2	5.29**			4.49**		5.00**
A. ballerus	3				0.42 ns	1.49 ns	
	4			7.44**			0.59 ns
R. rutilus	5			4.81**			1.16 ns
	6				4.39**	8.75**	

(Sars) were produced by sequential sieving through a set of sieves (500, 300, and 200 μm). The two size groups had a mean length of 0.49 mm (±0.053 SD, $n = 100$) and 0.65 mm (±0.109 SD, $n = 100$), respectively.

The cylindrical side walls of the experimental tanks were made of white plastic with diameters varying with fish sizes (Table 1). The glass bottoms of the tanks were covered by a sheet of blue graph paper. The experimental tanks were illuminated by a 15-V, 150-W halogen lamp (Philips No 6423) placed 60 cm overhead. Light intensity at the water surface was 12 000 lx. Fish were photographed from overhead with a black/white video camera with a 1.7-cm tube (JVC TK-122) so that fish could be seen from a dorsal view; the graph paper was visible in the background. Records were made with a U-matic video system (JVC portable CR-4400 E, CCIR-monochrome system, 320 horizontal lines, 50 frames·s^{-1}).

Fish were starved 24 h before the experiments in vessels identical to the experimental tank. Groups of three individuals were used in the experiments, because it was obvious from pilot experiments that single fish showed disturbed feeding behaviour. Thirty minutes before each feeding, three starved fish were introduced into the tank and allowed to adjust. One individual prey of a known size class was pipetted in, outside of the fish's reactive field (as established in pilot experiments), and attacks initiated by any of the three fish were recorded. Only those attacks in which prey was more than 50 mm from the side walls and in which reactions were preceded by a period of search were included in the analysis of RD. To prevent satiation, only 10–30 prey individuals (depending on fish size) were added in one experiment. Subsequently, the swimming path of one randomly chosen fish, without any prey present in the tank, was recorded for 1 min. These videographs were used for the analysis of average cruising speeds. Each type of experiment was replicated using different groups of fish.

Reactions to a prey item could be determined accurately by a sudden change in swimming direction and/or an acceleration, followed by attack and consumption of prey. In the moment of reaction the coordinates of the prey (A) as well as the snout (B) and tail of the fish (C) were determined (Fig. 1a). From the coordinates the following parameters were calculated:

Reactive distance (RD) = length of vector A − B (a)
Standard length (SL) = length of vector B − C (b)
Reaction angle (RA) = 180 − arc cos ($a \cdot b / |a| \cdot |b|$)

With RD and prey size (h), the visual angle of the fish was calculated (see Fig. 1b):

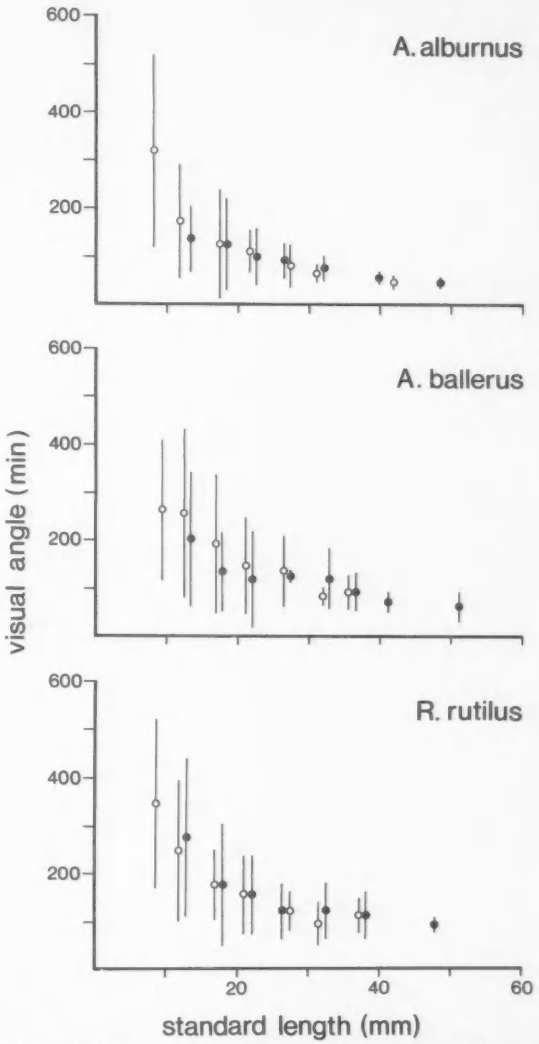

FIG. 3. Mean visual angles versus standard length. Closed circles: mean visual angle for *Ceriodaphnia reticulata* (0.65 mm body length); open circles: mean visual angle for *Ceriodaphnia reticulata* (0.49 mm body length). Vertical bars represent ±1SD.

$$\text{Visual angle (VA)} = 2 \cdot (\arctan (0.5 \cdot h/\text{RD}))$$

The average cruising speed was determined from short, straight lines of the swimming path. The coordinates of the fish's snout at the beginning and at the end of the line were recorded together with the elapsed time.

Experiments were carried out at weekly intervals during the first 3 mo after hatching. Water temperature in the experiments was 20°C (±1°C). All experiments were carried out between 0900 and 1700 h.

Results

A linear relationship between reactive distance and fish size was observed in all three species with both size classes of prey (Fig. 2). In order to test the linearity of the relationships and

TABLE 3. Analysis of covariance of regression relating visual angles to standard length. Tested are regressions for two prey size classes per species. Values above the diagonal refer to slopes, below the diagonal to intercepts. Values marked **: significance level = 0.05; ns = not significant on the 0.05 level.

Regression No. test for linearity		*A. alburnus* 1	2	*A. ballerus* 3	4	*R. rutilus* 5	6
	(*F*)	0.61**	7.98 ns	0.76**	1.12**	1.13**	0.44**
Regression No.							
A. alburnus	1		1.96 ns				
	2	0.85 ns					
A. ballerus	3				1.35 ns		
	4			0.11 ns			
R. rutilus	5						1.67 ns
	6					1.09 ns	

possible differences, an analysis of covariance (Lindner and Berchthold 1982) was performed. Significant differences in the elevation of regression lines for different prey sizes were found in all species, while the slopes proved to be similar (Table 2). From RDs and prey sizes, visual angles (Breck and Gitter 1983) can be calculated (Fig. 3). The accuracy of the RD determinations is indicated by the identity of the visual angles calculated for the two prey size classes (for a statistical evaluation see Table 3).

Figure 4 shows the frequency distribution of reaction angles, i.e. the angle between the fish's longitudinal axis and the prey at the moment of reaction (see Fig. 1a). Maxima between 30 and 60° are evident in all three species. Not only were most reactions observed in this range, but visual acuity was also higher as indicated by slightly lower visual angles (Table 4). These differences, however, are not statistically significant (Mann–Whitney *U*-test, $p = 0.05$).

So far only limited data on average cruising speeds have been gathered. Linear relationships between cruising speed and standard length were developed for all three species as a first approximation (Fig. 5).

From RDs and average cruising speeds, theoretical prey location volumes per unit time have been calculated as a cylinder with radius = RD and height = average cruising speed (Confer et al. 1975; Eggers 1977). Because of the characteristics of the visual field (see Fig. 4 and Table 4), a correction was made for the radius in the following way: frequency distributions of reaction angles define the probability that attacks are performed in a certain direction. Thus it seems reasonable to compute the mean RDs of reactions within that range where the probability for reactions is highest (here between 0 and 70°, probability >0.7). At least for a cruising predator, the mean RD should be projected to the transversal plane to determine the radius required for computing the prey location volume (see Fig. 1a). Using this correction, the radius of the cylinder is reduced only slightly compared with simply taking the mean RD for computation. Prey location volume, however, becomes 12–25% lower.

Figure 6 shows the ontogenetic development of calculated prey location volume of the three species for a prey size of 0.5 mm.

Interspecific differences in the development of visual acuity, expressed either as RD (Fig. 2) or as visual angles (Fig. 3 and 7) are evident. Above a size of 20 mm, RDs were higher in bleak than in roach. Values for blue bream are intermediate (see Fig. 2 and 3; Table 2 and 3). The same holds true for interspecific differences in cruising speeds (Fig. 5).

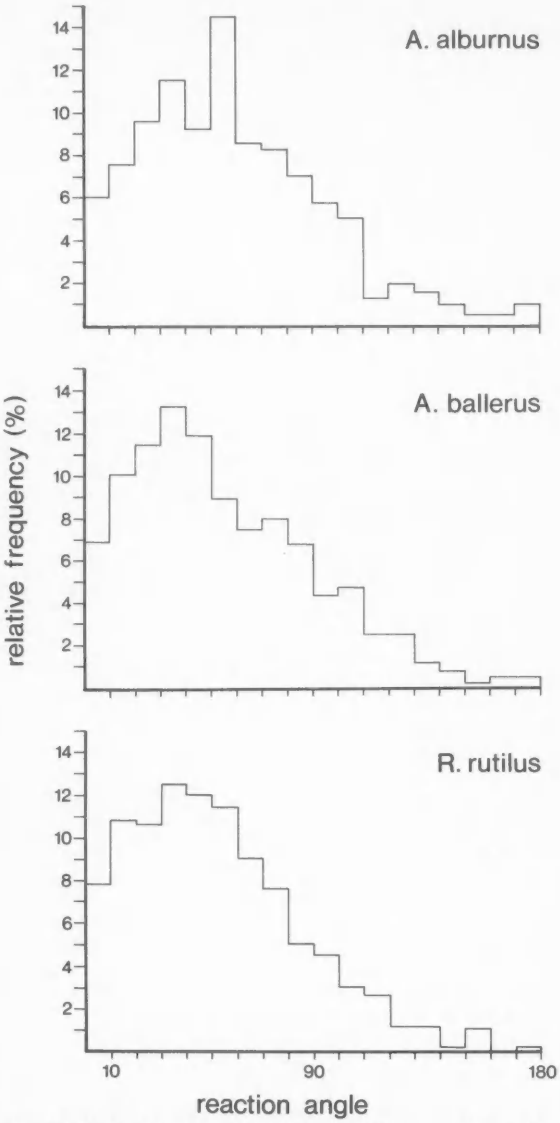

FIG. 4. Relative frequency of reactions at different reaction angles. Frequency distributions for the three species are statistically not different (Kolmogorov–Smirnoff test: *A. alburnus* versus *A. ballerus*: $D = 0.039$, $p < 0.01$; *A. alburnus* versus *R. rutilus*: $D = 0.058$, $p < 0.01$; *A. ballerus* versus *R. rutilus*: $D = 0.025$, $p < 0.01$).

Figure 7 provides an overview of major interspecific differences. The graph compares visual acuity and average cruising speeds of fish >25 mm standard length. Visual acuity is highest in bleak as indicated by lowest mean visual angle (mean visual angle = 85.3 min, SD = 37.8, $n = 61$). It is 18% lower in blue bream (mean visual angle = 104.1 min, SD = 39.0, $n = 109$) and 28% lower in roach (mean visual angle = 118.5 min, SD = 41.6, $n = 94$). These interspecific differences of visual angles are statistically significant (Mann-Whitney *U*-test: *A. alburnus* versus *A. ballerus*: $Z = -3.112$, $p < 0.01$; *A. alburnus* versus *R. rutilus*: $Z = -4.909$, $p < 0.01$; *A. ballerus* versus *R. rutilus*: $Z = -2.623$, $p < 0.01$). Cruising speeds are

TABLE 4. Mean visual angles (± standard deviations and numbers of observations) at different ranges of reaction angles.

Species	Reaction angle	Visual angle		
		Mean	SD	*N*
A. alburnus	0–30	94.1	34.5	13
	30–60	87.9	39.1	27
	60–90	93.1	45.1	18
A. ballerus	0–30	121.6	50.6	33
	30–60	115.6	56.0	49
	60–90	123.7	81.6	40
R. rutilus	0–30	123.8	47.9	29
	30–60	113.8	36.7	39
	60–90	126.9	52.0	29

calculated using the equations given in Fig. 5 for fish of 30 mm standard length.

Discussion

The analysis of prey detection capacity is important in understanding the foraging ecology of a species. Visual acuity and the characteristics of the visual field are key parameters in defining prey location volumes which can influence prey selection. The influence of the visual field for computing the prey location volume was first investigated by Confer et al. (1978). Recent attempts to define the influence of the visual field on prey location volumes have been made for bluegill sunfish (Luecke and O'Brien 1981) and for coho salmon (Dunbrack and Dill 1984). The latter authors suggested that RDs should be weighted according to frequencies of attacks; this is in accordance with our results.

Furthermore, the visual field is important for prey selectivity because it influences the ability to recognize absolute prey size. The characteristic frequency distribution of reaction angles indicates the visual field of the fish in the horizontal plane. The low frequencies directly in front of the fish correspond well with results for adult herring (Blaxter and Jones 1967), coho salmon (Dunbrack and Dill 1984), and bluegill sunfish (Luecke and O'Brien 1981). Braum (1964), in a study based on histological measurements and analysis of films, proposed a "blind region" directly in front of larval coregonids and pike while searching for prey. Binocular vision is only achieved during attacks on individual prey items when the eyes are oriented forward. We therefore conclude that young cyprinids have no binocular vision when searching for prey and thus have a limited recognition of absolute prey size.

The increase in visual acuity during ontogenesis can be explained by the growth of the eye and the development of signal integration (e.g. the optic tectum). Anatomical and optical measurements carried out by Tamura and Wisby (1963) established that visual acuity depends to a large extent on eye lens diameter and cone density of the retina. Blaxter and Jones (1967); Johns and Easter (1977); and Breck and Gitter (1983) argued that, due to the growth of the lens, acuity increases in growing fish despite a decrease in cone density. This means that a given object at a fixed distance casts a larger image in a larger eye.

Interspecific differences in visual acuity may also be explainable by possible differences in eye dimensions and integrating systems. A third parameter in importance could be the spherical aberration of the crystalline lenses of fish. Spherical aberration is highly correlated with foraging modes (Kreuzer and Sivak 1984). Visually oriented, predatory fish have low while omnivorous fish have high spherical aberrations. Srocinsky (1977), for example, found that spherical aberration is high in roach compared with other species. This could be a reason why bleak — as a more visually oriented fish species — have higher RDs.

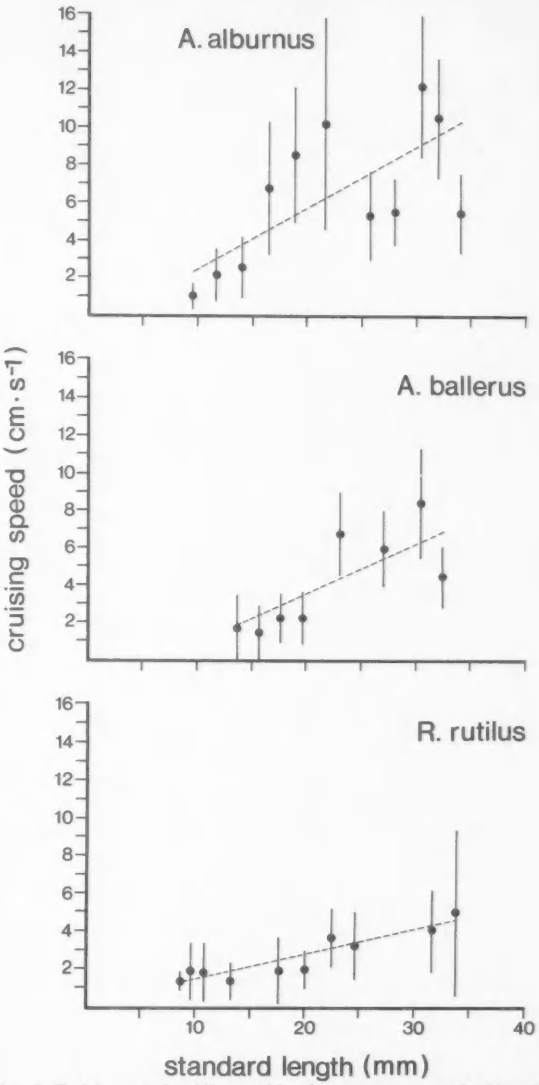

FIG. 5. Cruising speeds while searching for prey versus standard length of fish. Symbols represent mean cruising speed of one fish during 1 min. Vertical bars indicate ± 1SD.
Regression equations:
A. alburnus: $V = -0.58 + 0.32 \cdot SL$, $r = 0.58$, $n = 732$;
A. ballerus: $V = -2.0 + 0.28 \cdot SL$, $r = 0.57$, $n = 390$;
R. rutilus: $V = 0.13 + 0.13 \cdot SL$, $r = 0.49$, $n = 610$.

Although larval and juvenile fish of the three species are almost exclusively planktivorous (Panova 1966; Cryer et al. 1986; Mark et al. 1987; Keckeis et al. 1988), distinct differences in their abilities to detect planktonic prey are evident. These differences coincide to some extent with the trophic specialization of the adults. The highest RDs of juvenile bleak cor-

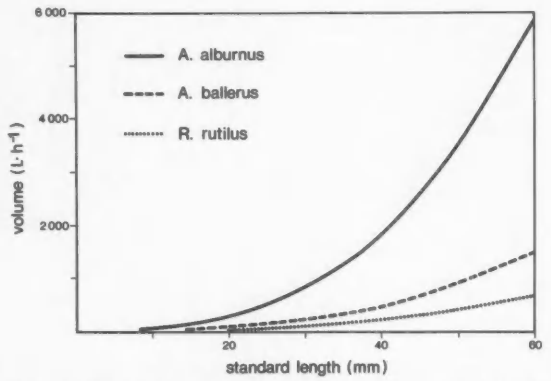

FIG. 6. Theoretical prey location volumes per time versus standard length. Values are based on RD measurements in the horizontal plane.

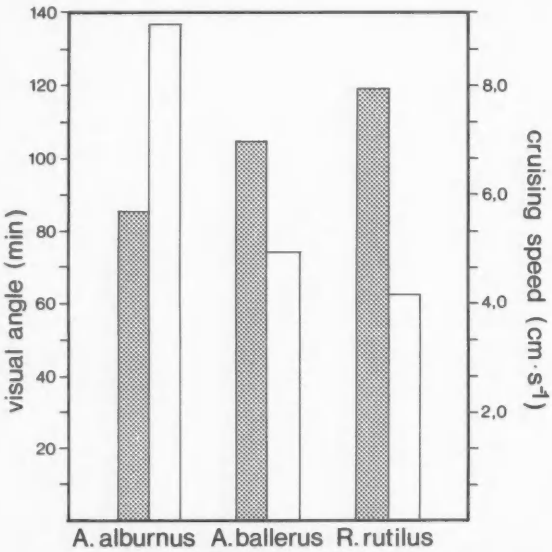

FIG. 7. A comparison of visual angles of fish >25 mm standard length and cruising speeds calculated for fish of 30 mm standard length using the equations given in Fig. 5. For statistics see text.

relate with the visually oriented foraging mode of adult bleak, while the omnivorous feeding mode of adult roach corresponds with lowest RDs of the juveniles. These differences indicate that morphological differentiation, for example of the visual apparatus (Braum 1964; Blaxter and Jones 1967), is already far advanced in fish above 20 mm standard length.

The differences in prey detection capacities during the ontogenetic development as well as between species have considerable effects on the foraging site selection in 0+ cyprinids (Schiemer et al. 1989; Mark et al. 1987).

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Evaluating Fisheries Management Models by Simulated Adaptive Control — Introducing the Composite Model

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This paper uses the technique of simulated adaptive control to provide a method for comparing the performance of different fisheries management models. The management model is evaluated not in isolation, but rather as part of an integrated fisheries management system which includes the simulated population dynamics of the exploited fish, the simulated fishery, the fishery management policy formulation process, and the analysis of the simulated fisheries data. The technique is used to compare a simple biomass dynamic based model introduced by Ludwig and Hilborn with a more complicated length-based model developed by Fournier and Doonan. A composite model which combines the biomass dynamic based model with the length-based model was also evaluated. The composite model performed better than either of its component models.

Dans le présent document, les auteurs utilisent la technique de la simulation du contrôle d'adaptation pour obtenir une méthode de comparaison du rendement des différents modèles de gestion des pêches. Le modèle de gestion est évalué non pas isolé, mais plutôt dans le cadre d'un système intégré de gestion des pêches qui comprend la dynamique simulée des populations du poisson exploité, la pêche simulée, le processus de formulation de la politique de gestion des pêches et l'analyse des données des pêches simulées. La technique est utilisée pour comparer un modèle simple reposant sur la dynamique de la biomasse introduit par Ludwig et Hilborn à un modèle plus compliqué reposant sur la longueur mis au point par Fournier et Doonan. Un modèle composite qui combine le modèle fondé sur la dynamique de la biomasse au modèle reposant sur la longueur a également été évalué. Le modèle composite a donné de meilleurs résultats que les modèles utilisant l'un de ses composantes.

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The ability of computer simulation methods to investigate the behavior of complex systems is well established. Aeronautical engineers, for example, use them to design and simulate the flight of new types of aircraft, thereby avoiding the necessity for building costly prototypes. Simulation methods promise to be extremely valuable for investigating the behavior of management systems for fisheries. Unlike airplane design where at least in principle many different planes can be built, a fishery can be managed only once and results are obtained only after perhaps decades. To investigate the possible outcomes under different management systems it is necessary to resort to computer simulation.

A managed fishery presents a collection of complicated interactions between the biological dynamics of the exploited species, the economic forces on the fishing fleet, the methods used by managers for analyzing the fishery, and the methods used by managers for policy implementation. The developers of models for fisheries management have tended to concentrate on the biological dynamics of the fish and to ignore the other components of the fishing process. In keeping with this point of view the performance of a fisheries management model is usually evaluated by applying it to a time series of real or simulated fisheries data and producing estimates of parameters describing such things as growth, mortality, or total biomass. The model is then judged by the perceived accuracy of such estimates. While this approach may be valuable in the early development stages of a fisheries management model, it has not led to an understanding by managers of how a particular model might function in practice.

Managing a fishery is not a static process where a model is used once and a policy decision based on the analysis is made. It is a dynamic and ongoing process. A fisheries model is used many times, in a series of analysis, policy formulation, fishery exploitation, and data gathering steps. The fisheries manager is not especially interested in whether the model produces good estimates of growth or mortality in a particular year. Instead, he or she wants to know what the outcome of a number of policy decisions over a number of years is likely to be. Such outcomes are the result of a series of complicated interactions. Simulation methods are ideal for studying these situations.

An indication of the ability of simulation methods to investigate the behavior of fisheries management systems is the result obtained by Ludwig and Walters (1985). They simulated the management of an exploited fish population whose dynamics

followed the assumptions of a model proposed by Deriso (1980). They employed a simple model developed in Ludwig and Hilborn (1983) as well as Deriso's more complicated model to analyze a time series of catch and effort data from the simulated fishery. Results from the two different analyses were used to formulate adaptive control policies which were applied to the fishery in the next time period. This process was repeated over a number of years and the cumulative results compared. They reported that better results were obtained by using the simple model rather than Deriso's more complex model even though the data were generated exactly according to the assumptions of Deriso's model. This is a remarkable result, and certainly not one which would be anticipated by simply examining the models themselves.

The fact that simple models may perform better than more complicated models in fishery management systems illustrates a common aspect of mathematical modelling. As models become more complicated they are more likely to exhibit unpredictable behavior. Such situations seem to be the rule rather than the exception. This has led to an extreme reluctance by managers to accept new products of the modeler's art.

The need to design fisheries models that exhibit stable behavior when used with real fisheries data is related to the notion of robustness in statistical parameter estimation. Roughly speaking, a parameter estimation scheme is said to be robust if it is insensitive to large deviations from the model's hypotheses. As it is widely believed that real fisheries data and real fisheries always exhibit large deviations from any model's hypotheses, this question of robustness is of paramount importance to fisheries managers. The manager wants to know whether it is possible that some unsuspected deviation from the model's hypotheses will lead to disastrous policy decisions if the model is used for analysis. The job of the modeler is to produce a model which gives acceptable performance over a broad range of situations which represent deviations from the model's hypotheses. To achieve this stability he or she is willing to use an estimation scheme which is somewhat less efficient in the case where the model's hypotheses are satisfied exactly. We shall introduce a general method for improving the robustness of certain types of statistical models of interest in fisheries management. The method can be adjusted to make the model more or less robust. As the model is made more robust it becomes less sensitive to the errors in 'bad' data. Of course it also becomes less able to extract the information which might be present in 'good' data. The goal is to find a level of robustness which produces a model which can use data with large errors but which is still useful in a fisheries management system.

The method which we shall use to investigate the performance of fisheries management models is simulated adaptive control. Each iteration of the simulated adaptive control procedure consists of three stages: a fishery simulation stage, an analysis stage, and a policy formulation stage. In the fishery simulation stage the fish population is generated according to the assumed dynamics which control its evolution, the fish population is exploited according to the policy determined at the previous iteration, and data from the fishery are generated for the analysis stage. Stochastic deviations or "chance errors" can be incorporated into the model at this stage. These include random deviations in the stock–recruitment relationship, random deviations in the relationship between estimated fishing effort and the actual level of fishing mortality, random age-dependent deviations in fishing mortality and sampling errors in the data gathered from the simulated fishery.

In the analysis stage the simulated data from the fishery are analyzed and parameter estimates are produced which describe the current state of the fish stock. In the policy stage the parameter estimates from the analysis stage are used to formulate the fishing policy for the next period. This policy is then incorporated into the simulation model and the whole procedure is repeated for another fishing period. After a certain number of iterations of the procedure the results are tabulated and compared for different fishing analysis models.

There are many criteria which can be used to evaluate the performance of a fisheries management model. As one measure of performance we have used the total weight of the catch taken during the 60-yr simulated management period. Alternatively one could use the total discounted catch using some nominal discounting rate.

Of course it is not possible to separate the model evaluation criterion from the policy which is used to determine the catch quota. With a high discount rate, the policy which produces the largest discounted average yield would hold the biomass at a much lower level than the policy which produces the largest average yield. This point can not be overemphasized. It is essential that the policy used for management, the criterion used for model evaluation, the fisheries management model, and the population dynamics of the exploited population be considered as a whole.

We have adopted a control policy which is similar to what is often practiced in fisheries management. Under this policy the quota is increased or decreased slightly from year to year depending on whether the stock is perceived to be above or below the optimal level. The policy is based on the concept of maximum sustainable yield. For each year the catch data are analyzed and the biomass level which would produce the maximum equilibrium yield is estimated. In addition the biomass level for the next year is estimated. If the estimated biomass level for the next year is greater than the present estimate of the optimal equilibrium biomass level, the quota is increased. If the estimated biomass level is less than the estimate of the optimal equilibrium biomass level, the quota is decreased.

In order to perform well the management model does not need to produce a good estimate of the optimum equilibrium biomass level or a good estimate of the biomass for the next year. Roughly speaking, it is only necessary that the fisheries management model be good at producing an estimated biomass level for the next year which is on the correct side of the estimated optimal biomass level so that the quota is increased or decreased at the opportune moment.

Ludwig and Walters (1985) suggested that the reason why their simple model performed better than Deriso's more complicated model is that catch and effort data simply do not contain enough information to enable the estimation of the larger number of parameters present in Deriso's (1980) model. We thought that the superiority of the Ludwig–Hilborn (1983) model (LH model) might be due to its ability to make correct forecasts rather than its ability to estimate model parameters. If the more complicated model produced better estimates of the parameters describing the stock dynamics while the LH model performed better due to its superior ability to make forecasts, we reasoned that a composite model made up of both the LH model and the more complicated model might perform better than either model alone. For the more complicated model we have used the model of Fournier and Doonan (1987) who extended the techniques used in Deriso's (1980) model to

develop a model which could incorporate length and weight data from a fishery as well as catch and effort data.

To illustrate how computer simulation methods can be used to investigate the performance of fisheries management models we shall use simulated adaptive control to compare the performance of the Fournier–Doonan (1987) model (FD model), the LH model, and a composite model formed from the FD and LH models (FD–LH model) for two scenarios of interest to fisheries managers. As we shall show, the LH model performs about as well as the FD model in the cases considered in this paper, while the FD–LH model performs better than either of its component models. Such composite models are an interesting new class of models to study for fisheries management applications.

To obtain an estimate of how well the models are able to furnish parameter estimates for implementing fisheries management policies, the optimal policies were also calculated for the situation where all the parameters in each year were known without error. This situation is referred to as the PI (perfect information) model. The results obtained for the PI model are the best obtainable under the policy employed.

The following list contains a description of the symbols used to define the models in this paper. Symbols which are used in more than one model only appear once.

LH Model

Y The number of years of fishing data,
i indexes years of fishing data,
B_i the biomass in year i,
C_i the catch in year i,
C_i^{obs} the observed catch in year i,
δ_i random variable generating the random deviations in the observed catch–true catch relationship in year i,
σ_δ^2 the variance of the random variables δ_i,
S_i the survival rate from fishing in year i,
E_i the effective fishing effort in year i,
E_i^{obs} the observed fishing effort in year i,
ϵ_i random variable generating the random deviations in the observed effort–effective effort relationship in year i,
σ_ϵ^2 the variance of the random variables ϵ_i,
D_i the deviation from the effective effort in year i,
q the catchability,
α, β parameters which determine the stock dynamics,
$\tilde{B}(S)$ the equilibrium biomass level for survival rate S,
B^{opt} the equilibrium biomass level which produces the largest equilibrium catch,
S^{opt} the survival rate which produces the largest equilibrium catch,
B^{proj} the projected biomass level in the year $Y+1$,
Q_i the fishing quota for year i.

FD Model

j Indexes age classes or year groups,
n_i the number of fish sampled from the catch in year i,
N_{ij} the number of age j fish in the population in year i,
$N_{i\cdot}$ the total number of fish in the population in year i,
k the age of recruitment,
R_i the number of recruiting age k fish in year i,
l the survival rate (from natural mortality) in year i,
α_{FD}, β_{FD} parameters determining the form of the stock–recruitment relationship,
η_i random variable generating the random deviations in the stock–recruitment relationship in year i,
σ_η^2 the variance of the random variables η_i,
H_i the random component of recruitment in year i,
τ_j the mean length of the age j fish,
w_j the mean weight of the age j fish,
a mean length of the age 1 fish,
ρ parameter in the von Bertalanffy growth curve,
b parameter in the weight–length relationship,
σ_L^2 the variance of the length distribution of the age j fish (the same for all j),
μ_{ir} the rth central moment of the length distribution of the population in year i,
λ_i^r the rth noncentral moment of the length distribution of the population in year i,
κ_{i3} the skewness of the length distribution of the population in year i,
κ_{i4} the kurtosis of the length distribution of the population in year i,
M_i the mean weight of the fish in the population in year i
M_{i2} the variance of the weight distribution of the fish in the population in year i,
$\tilde{R}(S)$ the equilibrium level of recruitment at survival rate S,
$\tilde{N}(S)$ the equilibrium total number of fish at survival rate S,
$\tilde{\mu}^r(S)$ the equilibrium value for the rth central moment of the length distribution at survival rate S,
$\tilde{\lambda}^r(S)$ the equilibrium value for the rth noncentral moment of the length distribution at survival rate S,
N_j^{proj} the projected number of age j fish in year $Y+1$.

FD–LH Model

ζ_i Random variable generating the deviations from the LH dynamics in year i.

A $\hat{}$ over any symbol is used to denote an estimate for that parameter. For example $\hat{q}$ is the estimated catchability and $\hat{S}^{opt}$ is the estimated optimal biomass level.

Structure of the LH Model

Our implementation of the LH model is determined by the following equations.

$$(1.1)\quad B_i = \alpha S_{i-1} B_{i-1} \exp(-\beta(B_{i-1}/B_1 - 1))$$

$$(1.2)\quad S_i = e^{-qE_i}$$

$$(1.3)\quad C_i = (1 - S_i) B_i$$

$$(1.4)\quad E_i = E_i^{obs} e^{\epsilon_i}$$

$$(1.5)\quad C_i = C_i^{obs} e_i^{\delta}$$

Equation (1.1) describes the dynamics of the population. Equations (1.2) through (1.5) describe the relationship of the fish population to the fishery and the observed data E_i^{obs} and C_i^{obs}. The ϵ_i and δ_i are normally distributed random variables with variances δ_ϵ^2 and σ_δ^2 and with means $-\sigma_\epsilon^2/2$ and $-\sigma_\delta^2/2$. The relative sizes of the variances of the ϵ_i and δ_i determine whether the model parameters should be estimated in such a fashion that C_i is close to C_i^{obs} or so that E_i is close to E_i^{obs}.

Equilibrium Calculations for the LH Model

To formulate the policies used in the simulations it is necessary to estimate the equilibrium biomass level which produces the largest equilibrium catch, and also to forecast the biomass at the beginning of the next fishing period. Let $\tilde{B}(S)$ denote the equilibrium biomass level for a survival level S from fishing. The unfished equilibrium biomass level $\tilde{B}(1)$ satisfies the equation

$$\tilde{B}(1) = \alpha\tilde{B}(1)\exp(-\beta(\tilde{B}(1)/B_1 - 1))$$

it follows that

$$B_1 = \tilde{B}(1) \quad \text{if and only if} \quad \alpha = 1.$$

Thus the condition that the biomass was at the unfished equilibrium level in year 1 is equivalent to setting $\alpha = 1$. In general for a fixed level of survival S, the corresponding equilibrium biomass level $\tilde{B}(S)$ satisfies the relationship

$$\tilde{B}(S) = \alpha S\tilde{B}(S)\exp(-\beta(\tilde{B}(S)/B_1 - 1))$$

or

$$(1.6) \quad \tilde{B}(S) = \frac{B_1}{\beta}(\beta + \ln(\alpha S))$$

The survival rate S^{opt} at which the maximum equilibrium yield is obtained is found by solving the maximization problem

$$\max_S \{(1-S)\tilde{B}(S)\} \quad \text{or} \quad \max_S \left\{\frac{B_1}{\beta}(1-S)(\beta + \ln(\alpha S))\right\}$$

numerically. The corresponding optimal equilibrium biomass level B^{opt} is then determined by

$$B^{opt} = \tilde{B}(S^{opt})$$

Biomass Projections for the LH Model

B^{proj}, the estimated biomass projection in year $Y+1$ is given by

$$(1.7) \quad B^{proj} = \hat{\alpha}\hat{S}_Y \hat{B}_Y \exp(-\hat{\beta}(\hat{B}_Y/\hat{B}_1 - 1))$$

Parameter Estimation for the LH Model

The parameters for the LH model are estimated by minimizing an objective function whose form is adapted to the nature of the probabilistic errors occurring in the data and model processes. Recall that Y denotes the number of years data. To carry out the estimation process we first pick a set of fundamental parameters. This is a subset of all the model parameters in terms of which all the other model parameters can be expressed. For the LH model a fundamental set consists of the parameters B_1, q, α, β, and the quantities D_i for $i = 1,\ldots,Y$, which serve to represent the deviations between the observed effort E_i^{obs} and the effective effort E_i. The relationship is

$$(1.8) \quad E_i = E_i^{obs} e^{D_i}.$$

D_i is a model parameter which is equal to the value taken by the random variable ϵ_i in year i.

The parameters are calculated in terms of the fundamental parameters as follows. Calculate the effective efforts E_i in terms of the E_i^{obs} and the D_i by equation (1.8). Calculate the survival rates S_i from equation (1.2). Calculate the biomass B_i in each year from equation (1.1). Finally, calculate the catches C_i in each year from equation (1.3). The parameters are then estimated by solving the minimization problem.

$$(1.9) \quad \min_{B_1,q,\alpha,\beta,D_i} \left\{p_0 \sum_i (\ln(C_i) - \ln(C_i^{obs}))^2 + p_1 \sum_i D^2\right\}$$

The quantities p_0 and p_1 are not estimated in the model, but are preset. The parameter estimates obtained by minimizing (1.9) depend on the ratio p_0/p_1. This is a nonlinear analogue of the classical "errors in variables" problem (Kendall and Stuart 1958). For such a problem it is known that the ratio p_0/p_1 can not be estimated from the data — they must be determined externally. Fortunately many problems provide such additional information.

The "best" value to use for the ratio p_0/p_1 is the variance ratio $\sigma_\delta^2/\sigma_\epsilon^2$. If both the errors in catch and effort are sufficiently small, the model will simply fit the data and the parameter estimates will not depend significantly on the ratio p_0/p_1. Also if the errors in the estimated catches is large the model will not provide good estimates for management. (You have to know the catches. Otherwise you shouldn't be analyzing the data, you should be designing a better catch sampling scheme.) If the variance, σ_δ^2, in the estimated catch errors is larger than 0.01 the catch data are suspect.

We have generated data for which there are large deviations between the observed and effective effort ($\sigma_\epsilon^2 = 0.25$) and no error in the estimated catches. An analysis of the catch per unit effort data for the fishery reveals that either the biomass abundance fluctuates wildly from year to year or there is a large random component to the observed effort–effective effort relationship. A biologist would be aware that there are at least several age classes in the fishery for the species being simulated in this paper. For a population with several age classes the biomass can not exhibit such large fluctuations from one year to the next. Therefore there must be a large random component in the observed effort–effective effort relationship. We have used a ratio of 35.7 for p_0/p_1.

FD Model

Fournier and Doonan (1987) developed a general theory of fisheries models which include models of varying complexity. In this paper we shall consider the simple knife-edged recruitment model in which fish recruit to the fishery at age k and all older age classes are equally vulnerable to the fishery.

The model is determined by equations (2.1) through (2.11).

$$(2.1) \quad N_{ik} = R_i$$

$$(2.2) \quad N_{ij} = lS_{i-1} N_{i-1,j-1} \quad \text{for } j>k$$

$$(2.3) \quad R_i = \alpha_{FD} N_1 . e^{\eta_i} \quad \text{for } 2\leq i\leq k$$

$$(2.4) \quad R_i = \alpha_{FD} N_1 . B_{i-k}/B_1 \exp(-\beta_{FD}(B_{i-k}/B_1 - 1))e^{\eta_i} \quad \text{for } i\geq k+1$$

$$(2.5) \quad \tau_j = a(1-\rho^j)/(1-\rho) \quad \text{where } 0<\rho<1$$

$$(2.6) \quad w_j = b\tau_j^3$$

$$(2.7) \quad B_i = \sum_{j\geq k} w_j N_{ij}$$

$$(2.8) \quad S_i = e^{-qE_i}$$

$$(2.9) \quad C_i = (1 - S_i)B_i$$

$$(2.10) \quad E_i = E_i^{obs} e^{\epsilon_i}$$

(2.11) $C_i = C_i^{obs}\, e^{\delta_i}$

It is assumed that the lengths of the age j fish are normally distributed around their mean τ_j with variance σ_L^2.

Equations (2.1) through (2.4) describe the dynamics of the fish population in terms of numbers of fish. All age classes are assumed to experience the same fishing mortality in each year, i.e. there is no age-dependent selectivity in the fishery. The biomass of the fish B_i enters into the Ricker stock–recruitment relationship in equations (2.3) and (2.4). We have employed α_{FD} and β_{FD} to distinguish them from the symbols α and β which are usually employed in this relationship because these symbols have already been used for the LH model. The η_i in equations (2.3) and (2.4) represent normally distributed random variables which are the random noise present in the stock–recruitment relationship. Because of the k year lag between the biomass B_i and the resulting recruitment R_{i+k}, the biomass producing the recruitment in year i for $2 \leq i \leq k$ is not available. The biomass in year 1 has been used instead (equation 2.3). Equation (2.5) states that the mean lengths τ_j of the age j fish lie on a von Bertalanffy growth curve where a is the mean length of the age 1 fish. Notice we make no assumption in this paper about how individual fish grow. Equation (2.6) states that the mean weight for each age class is proportional to the cube of the mean length for that age class.

Let μ_{ri} denote the rth central moment of the length distribution of the population in year and M_i denote the mean weight of the fish in the population in year i. Fournier and Doonan (1987) used the first four central moments in the parameter estimation procedure. The skewness and kurtosis have better statistical properties than the third and fourth central moments and we have employed them in this paper. The skewness κ_{3i} and kurtosis κ_{4i} are defined by

(2.12) $\kappa_{3i} = \mu_{3i}/(\mu_{2i})^{1.5}$ and $\kappa_{4i} = \mu_{4i}/(\mu_{2i})^2$

Parameter Estimation for the FD Model

Since all the fish in the population are equally vulnerable to the fishery, the length and weight distribution of the fish in the catch are equal to the length and weight distribution of the fish in the fishery. Assume that a random sample of the catch is taken in each year and let M_i^{obs}, μ_{ri}^{obs}, κ_{3i}^{obs}, and κ_{4i}^{obs} denote the values of these statistics for the sample. As with the LH model let the quantities D_i be equal to the deviations in effective effort so that

$$E_i = E_i^{obs}\, e^{D_i}$$

In addition let the quantities H_i be equal to the random deviations in recruitment so that

$$R_i = \alpha_{FD} N_1 . e^{Hi} \quad \text{for } 2 \leq i \leq k$$

$$R_i = \alpha_{FD} N_1 . B_{1-k}/B_1 \exp(-\beta_{FD}(B_{i-k}/B_1 - 1)) e^{Hi} \quad \text{for } i \geq k+1$$

Now assume for the moment that the weight of the catch and the moments of the length and weight distribution of the catch can be expressed in terms of the D_i, H_i, and a small number of parameters which we denote for the moment by Θ. A good candidate for an objective function whose minimum would determine the parameter estimates is the weighted least-squares estimator

$$\begin{aligned} \min_{D_i, H_i, \Theta} \Big\{ & p_0 \sum_i (\ln(C_i(\Theta)) - \ln(C_i^{obs}))^2 + p_1 \sum_i D^2 \\ & + p_2 \sum_i H_i^2 \\ & + p_3 \sum_i (\mu_{i1}(\Theta) - \mu_{i1}^{obs})^2 \\ & + p_4 \sum_i (\mu_{i2}(\Theta) - \mu_{i2}^{obs})^2 \\ & + p_5 \sum_i (\kappa_{i3}(\Theta) - \kappa_{i3}^{obs})^2 \\ & + p_6 \sum_i (\kappa_{i4}(\Theta) - \kappa_{i4}^{obs})^2 \\ & + p_7 \sum_i (M_i(\Theta) - M_i^{obs})^2 \Big\} \end{aligned} \tag{2.13}$$

Minimizing the objective function (2.13) provides a good method for estimating the model parameters D_i, H_i, and Θ when all the model's structural assumptions are satisfied, and the observed quantities μ_{i1}^{obs}, μ_{i2}^{obs}, κ_{i3}^{obs}, κ_{i4}^{obs}, and M_i^{obs} have normally distributed errors. However these statistics are highly sensitive to deviations from the models hypotheses. In addition, if the length or weight distribution is skewed, these statistics will have skewed distributions so that an estimation scheme based on minimizing (2.13) may also be sensitive to such deviations and lack robustness.

Fortunately there is a simple method for modifying an objective function such as (2.13) so that the estimation scheme becomes more robust. The method, which was first used by Wald (1940) to formulate a simple robust method for linear regression models, is implemented in the present situation by using an averaging process.

To illustrate the idea consider the time series of mean lengths μ_{i1}. For a positive integer g the μ_{i1}'s are split up into groups of size g and each group is replaced by its average. Since in general Y is not a multiple of g not all the groups can contain exactly g objects. The extra ones are put into the last group. Specifically let g be a positive integer and for the parameters μ_{ir}, let ${}_g\bar{\mu}_{jr}$ be defined by

$${}_g\bar{\mu}_{jr} = \sum_{i=(j-1)g+1}^{\min\{jg, Y\}} \mu_{ir}/g \text{ for } j \text{ satisfying } j > 0 \text{ and } (j-1)g + 1 \leq Y$$

Let J_g denote the maximum value of j satisfying $(j-1)g + 1 \leq Y$. For each value of g and Y, J_g is equal to the number of 'time-averaged' moments ${}_g\bar{\mu}_{jr}$. As g increases the average is taken over more and more members of the time series until $g = Y$ when the result is one time averaged moment which is simply the average of all the members of the time series.

Assume that the time-averaging procedure has been applied to the skewness, kurtosis, and mean weight time series as well as to their corresponding observed values calculated from the random sample of the catch. The parameters are estimated by solving the minimization problem (2.14).

$$\min_{D_i,H_i,\Theta}\Bigg\{p_0\sum_i(\ln(C_i(\Theta))-\ln(C_i^{obs}))^2+p_1\sum_i D_i^2$$

$$+p_2\sum_i H_i^2$$

$$+p_3\sum_{j=1}^{J_{g_1}}({}_{g_1}\bar{\mu}_{j1}(\Theta)-{}_{g_1}\bar{\mu}_{j1}^{obs})^2$$

$$+p_4\sum_{j=1}^{J_{g_2}}({}_{g_2}\bar{\mu}_{j2}(\Theta)-{}_{g_2}\bar{\mu}_{j2}^{obs})^2 \qquad (2.14)$$

$$+p_5\sum_{j=1}^{J_{g_3}}({}_{g_3}\bar{\kappa}_{j3}(\Theta)-{}_{g_3}\bar{\kappa}_{j3}^{obs})^2$$

$$+p_6\sum_{j=1}^{J_{g_4}}({}_{g_4}\bar{\kappa}_{j4}(\Theta)-{}_{g_4}\bar{\kappa}_{j4}^{obs})^2$$

$$+p_7\sum_{j=1}^{J_{g_5}}({}_{g_5}\bar{M}_j(\Theta)-{}_{g_5}\bar{M}_j^{obs})^2\Bigg\}$$

Note that the central moments, skewness, kurtosis, and mean weight time series have distinct averaging parameters g. The exact values used for the g's is discussed in the examples.

We will now demonstrate how the model's parameters, D_i, H_i, and Θ can be expressed in terms of a set of fundamental parameters. Let x_{ijy} denote the length of the yth fish from age class j in year i. We shall assume the lengths-at-age of the fish in each age class are normally distributed around their means with variance σ_L^2 independent of j so that

$$x_{ijy}=\tau_j+\epsilon_{ijy},$$

where the e_{ijy} have mean 0 and variance σ_L^2. Let λ_i^r denote the expected value of the rth noncentral moment of the length distribution of the population in year i. Then

$$\lambda_i^r=E\left\{\sum_{jy}(\tau_j+\epsilon_{ijy})^r\right\}\Big/\ N_i. \qquad (2.15)$$

where $E\{\ \}$ denotes the expectation operator. Expanding (2.15) by the binomial formula and using the linearity properties of the expectation operator one obtains

$$\lambda_i^r=\sum_{jy}\sum_{q=0}^{r}\binom{r}{q}\tau_j^{r-q}E\{\epsilon_{ijy}^q\}/N_i. \qquad (2.16)$$

where

$$\binom{r}{q}=\frac{r!}{q!(r-q)!}.$$

For the normally distributed random variables ϵ_{ijy}

$$E\{\epsilon_{ijy}\}=0\ E\{\epsilon_{ijy}^2\}=\sigma_L^2\ \ E\{\epsilon_{ijy}^3\}=0\ \ E\{\epsilon_{ijy}^4\}=3(\sigma_L^2)^2. \qquad (2.17)$$

Substituting (2.17) into (2.16) and simplifying the results we obtain the following equations.

$$\lambda_i^1=\sum_{j\geq k}\tau_j N_{ij}\Big/ N_i. \qquad (2.18)$$

$$\lambda_i^2=\left(\sum_{j\geq k}\tau_j^2 N_{ij}+\sigma_L^2\sum_{j\geq k}N_{ij}\right)\Big/\ N_i.$$

$$\lambda_i^3=\left(\sum_{j\geq k}\tau_j^3 N_{ij}+3\sigma_L^2\sum_{j\geq k}\tau_j N_{ij}\right)\Big/\ N_i.$$

$$\lambda_i^4=\left(\sum_{j\geq k}\tau_j^4 N_{ij}+6\sigma_L{}^2\sum_{j\geq k}\tau_j^2 N_{ij}+3(\sigma_L{}^2)^2\sum_{j\geq k}N_{ij}\right)\Big/\ N_i.$$

Derivation of the Difference Equations

Let the quantities T_i^r be defined by

$$T_i^r=\sum_{j\geq k}\tau_j^r N_{ij}. \qquad (2.19)$$

In terms of the T_i^r the relationships (2.18) become

$$\begin{aligned}\lambda_i^1&=T_i^1/N_{i\cdot}\\ \lambda_i^2&=(T_i^2+\sigma_L^2 N_{i\cdot})/N_{i\cdot}\\ \lambda_i^3&=(T_i^3+3\sigma_L^2 T_i^1)/N_{i\cdot}\\ \lambda_i^4&=(T_i^4+6\sigma_L^2 T_i^2+3(\sigma_L^2)^2 N_{i\cdot})/N_{i\cdot}.\end{aligned} \qquad (2.20)$$

From (2.6) and (2.7) it follows that the biomass B_i and the mean weight M_i satisfy the relationships

$$B_i=bT_i^3 \qquad (2.21)$$

and

$$M_i=bT_i^3/N_{i\cdot}\ . \qquad (2.22)$$

The central moments of the length distribution can be calculated from the noncentral moments using the relationships.

$$\begin{aligned}\mu_i^1&=\lambda_i^1\\ \mu_i^2&=\lambda_i^2-(\lambda_i^1)^2\\ \mu_i^3&=\lambda_i^3-3\lambda_i^2\lambda_i^1+2(\lambda_i^1)^3\\ \mu_i^4&=\lambda_i^4-4\lambda_i^3\lambda_i^1+6\lambda_i^2(\lambda_i^1)^2-3(\lambda_i^1)^4.\end{aligned} \qquad (2.23)$$

We have shown that mean weight and length moments of the catch can be expressed in terms of the $N_{i\cdot}$ and the T_i^r. It remains to show that the $N_{i\cdot}$ and the T_i^r can themselves be expressed in terms of a small number of parameters. To do this we shall show that they satisfy a first-order system of different equations. Now

$$N_{i\cdot}=\sum_{j\geq k}N_{ij} \qquad (2.24)$$

From equations (2.1) and (2.2) it follows that the $N_{i\cdot}$ satisfy the simple difference equation

$$N_{i\cdot}=lS_{i-1}N_{i-1,\cdot}+R_i \qquad (2.25)$$

For the T_i^r first note that from (2.5) it follows that the τ_j satisfy the relationship

$$\tau_j=\rho\tau_{j-1}+a.$$

Then

$$\begin{aligned}T_i^r&=\sum_{j\geq k}\tau_j^r N_{ij}\\ &=\sum_{j\geq k}(\rho\tau_j+a)^r lS_{i-1}N_{i-1,j}+\tau_k^r R_i.\end{aligned}$$

Using (2.19) this simplifies to

$$T_i^r=lS_{i-1}\sum_{p=0}^{r}\binom{r}{p}\rho^{r-p}a^p T_{i-1}^{r-p}+(a(1-\rho^k)/(1-\rho))^r R_i \qquad (2.26)$$

where T_i^0 has been used to denote $N_{i\cdot}$. Equations (2.25) and (2.26) form the desired system of difference equations.

Equilibrium Calculations for the FD Model

For a survival rate S from fishing let $\tilde{R}(S)$ be the equilibrium recruitment (in numbers of fish) and $\tilde{B}(S)$ be the equilibrium biomass level. Then using (2.4)

$$\tilde{R}(S) = \alpha_{FD}\tilde{N}_1.\tilde{B}(S)/B_1 \exp(-\beta_{FD}(\tilde{B}(S)/B_1 - 1)), \tag{2.27}$$

now

$$\tilde{B}(S) = \tilde{R}(S) \sum_{j\geq k} w_j(lS)^{j-k} \tag{2.28}$$

Eliminating $\tilde{R}(S)$ from (2.27) and (2.28) yields

$$\tilde{B}(S) = \frac{B_1}{\beta_{FD}}\left\{\beta_{FD} + \ln(\alpha_{FD}N_1 \cdot \sum_{j\geq k} w_j(lS)^{j-k}/B_1\right\}. \tag{2.29}$$

The equilibrium biomass level which produces the maximum equilibrium yield is found by solving the problem

$$\max_S\{(1 - S)\tilde{B}(S)\}$$

numerically for S^{opt} and setting $B^{opt} = \tilde{B}(S^{opt})$. To calculate the equilibrium values for the noncentral moments of the length distribution $\tilde{\lambda}^r(S)$ note that $\tilde{N}(S)$, the equilibrium number of fish, satisfies

$$\begin{aligned}\tilde{N}(S) &= \sum_{j\geq k} \tilde{R}(S)(lS)^{j-k} \\ &= \tilde{R}(S)/(1 - lS)\end{aligned} \tag{2.30}$$

while

$$\begin{aligned}\tilde{\lambda}^r(S) &= \sum_{j\geq k} \tau_j^r \tilde{R}(S)(lS)^{j-k}/\tilde{N}(S) \\ &\quad \sum_{j\geq k} \tau_j^r(lS)^{j-k}/(1 - lS)\end{aligned} \tag{2.31}$$

while the equilibrium values $\tilde{T}^r(S)$ can be calculated by

$$\tilde{T}^r(S) = \sum_{j\geq k} \tau_j^r \tilde{R}(S)(lS)^{j-k}. \tag{2.32}$$

If the stock is initially at equilibrium the stock–recruitment relationship (2.3) implies that

$$\tilde{R}(S) = \alpha_{FD}\tilde{N}(S)$$

so that

$$\alpha_{FD} = \tilde{R}(S)/\tilde{N}(S).$$

Using (2.30) if the stock is initially at unfished equilibrium, α_{FD} satisfies the relationship

$$\alpha_{FD} = 1/(1 - lS) \tag{2.33}$$

Biomass Projections for the FD Model

The estimated biomass B^{proj} in year $Y+1$ for the FD model is given by

$$B^{proj} = \sum_{j\geq k} \hat{w}_j N_j^{proj}$$

where

$$\begin{aligned}N_k^{proj} &= \hat{\alpha}_{FD}\hat{N}_1\hat{B}_{Y-k}/\hat{B}_1 \exp(-\hat{\beta}_{FD}(\hat{B}_{Y-k}/\hat{B}_1 - 1)) \\ N_j^{proj} &= \hat{l}\hat{S}_Y\hat{N}_{Y,j-1} \quad \text{for } j>k.\end{aligned}$$

From (2.21) and (2.26) it follows that

$$\begin{aligned}B^{proj} = \hat{b}\hat{l}\hat{S}_Y(\hat{\rho}^3\hat{T}_Y^3 + 3\hat{\rho}^2\hat{a}\hat{T}_Y^2 + 3\hat{\rho}\hat{a}^2\hat{T}_Y^1 + \hat{a}^3\hat{T}_Y^0) \\ + \hat{a}^3\left(\frac{1 - \hat{\rho}^k}{1 - \hat{\rho}}\right)^3 R^{proj}\end{aligned} \tag{2.34}$$

where

$$R^{proj} = \hat{\alpha}_{FD}\hat{N}_1.\hat{B}_{Y-k}/\hat{B}_1 \exp(-\hat{\beta}_{FD}(\hat{B}_{Y-k}/\hat{B}_1 - 1))$$

A set of fundamental parameters for the FD model consists of D_i, H_i, $N_{1\cdot}$, T_1^r for $r=1,\ldots,4$, a, ρ, b, σ_L^2, α_{FD}, and β_{FD}. If it is assumed that the model is initially at unfished equilibrium, the parameters $N_{1\cdot}$ and T_1^r are set equal to $\tilde{N}(1)$ and $\tilde{T}^r(1)$ and α_{FD} is set equal to $1/(1 - l)$. The model parameters are calculated iteratively year by year from this fundamental set as follows. In year 1, values for the parameters $N_{1\cdot}$, and T_1^r for $r=1,\ldots,4$ have been defined (this is trivial since they are part of the fundamental parameters or if the population is at unfished equilibrium they are defined in terms of other parameters). Now assume that all the model parameters up to year Y have been defined. To calculate the parameters in year $Y+1$ calculate R_i using (2.3) or (2.4)). Calculate $N_{Y+1,\cdot}$ using (2.25) and the T_{Y+1}^r using (2.26). Calculate the λ_{Y+1}^r using (2.20). Calculate the μ_{Y+1} using (2.23). Calculate B_{Y+1} using (2.21) and M_{Y+1} using (2.22).

Structure of the FD–LH Model

The FD–LH model does not have a deterministic structure. Instead it is assumed that both the FD and LH models give a valid description of the fisheries process and biological dynamics. Obviously this assumption can not be satisfied for deterministic models because the assumptions of the FD and LH models are inconsistent. However, since a fish population which evolves according to the assumptions of the FD model has a biomass level for which the expected yield is a maximum, it is possible that a simple biomass–dynamic model such as the LH model can provide an adequate approximate description of the population dynamics.

To make this notion precise, take the logarithm of both sides of equation (1.1) which describes the biomass–dynamics for the LH model. This gives equation (3.1) where the additional terms ζ_i are assumed to be independent normally distributed random variables with mean 0.

$$\ln(B_{i+1}) = \ln(\alpha) + \ln(S_i) + \ln(B_i) - \beta(B_i/B_1 - 1) + \zeta_i \tag{3.1}$$

The parameters of the FD–LH model are estimated by minimizing an objective function which incorporates both model assumptions simultaneously.

The objective function is

$$\begin{aligned}&p_0 \sum_i (\ln(C_i(\Theta)) - \ln(C_i^{obs}))^2 + p_1 \sum_i D_i^2 \\ &\quad + p_2 \sum_i H_i^2 \\ &+ p_3 \sum_{j=1}^{J_{g_1}} ({}_{g_1}\bar{\mu}_{j1}(\Theta) - {}_{g_1}\bar{\mu}_{j1}^{obs})^2 \\ &+ p_4 \sum_{j=1}^{J_{g_2}} {}_{g_2}(\bar{\mu}_{j2}(\Theta) - {}_{g_2}\bar{\mu}_{j2}^{obs})^2 \\ &+ p_5 \sum_{j=1}^{J_{g_3}} ({}_{g_3}\bar{\kappa}_{j3}(\Theta) - {}_{g_3}\bar{\kappa}_{j3}^{obs})^2\end{aligned} \tag{3.2}$$

$$+p_6 \sum_{j=1}^{J_{t_4}} ({}_{g_4}\bar{\kappa}_{j4}(\Theta) - {}_{g_4}\bar{\kappa}_{j4}^{obs})^2$$

$$+p_7 \sum_{j=1}^{J_{t_5}} ({}_{g_5}\bar{M}_j(\Theta) - {}_{g_5}\bar{M}_j^{obs})^2 \Bigg\}$$

$$+p_8 \sum_{i=1}^{Y-1} \Big(\ln(B_{i+1}) - \ln(\alpha) - \ln(S_i) - \ln(B_i) + \beta(B_1/B_i - 1)\Big)^2.$$

The difference between the objective function (3.2) and the objective function (2.14) is the addition of the final terms which incorporate the log-likelihood function corresponding to the assumption that the biomass tends to evolve according to the assumptions of the LH model as described by equation (3.1).

As $p_8 \to 0$ the parameter values which minimize (3.2) approach the parameter estimates which would be obtained by first minimizing (2.14) to obtain estimates $\hat{B}_i$ and $\hat{S}_i$ and then minimizing the sum of squares

$$\sum_{i=1}^{Y-1} \Big(\ln(\hat{B}_{i+1}) - \ln(\alpha) - \ln(\hat{S}_i) - \ln(\hat{B}_i) + \beta(\hat{B}_i/\hat{B}_i - 1)\Big)^2$$

with respect to α and β.

As $p_8 \to \infty$ the LH dynamics will dominate the estimation procedure. The best results were obtained for intermediate values of p_8. For the FD–LH model, the optimal biomass B^{opt} and the projected biomass level for the next year B^{proj} were calculated using equations (1.6) and (1.7).

Simulations

The data for the simulation runs were generated according to the hypotheses of the FD model in that equations 2.1–2.11 were used to generate the data.

Values of the parameters for the simulated fish population

Parameter	k	l	α_{FD}	β_{FD}	a	ρ	b	σ_L^2
Value	3	0.7	0.3	1.5	4.09	0.80	0.0596	4.0

The parameters have been chosen to produce a fairly slow growing fish with from five to eight significant age classes in the fishery. The variance, σ_η^2, of the random deviations in the stock–recruitment relationship was 0.16 and the variance, σ_ε^2, of the random deviations between observed and effective effort was 0.25.

For each year the mean length and weight data were produced by simulating a random sample of 400 fish.

For all the simulations the fish population is at its unfished equilibrium level in year 1. (Note however that for the second set of simulations the first 20 yr of fisheries data are discarded so that they are not available to the model.) The numbers describing the population dynamics were scaled so that the expected unfished equilibrium recruitment is equal to 200 fish. Of course the results obtained are independent of the scale factor used to determine the initial population size.

To give a feeling for the type of fish population which is being simulated, the following table gives the number of fish in each age class for the first year of the simulation as well as the mean length and mean weight of the fish in each age class.

Age	3	4	5	6	7	8	9	10	11	12	13
Number of fish	200	140	98	69	48	34	25	17	12	8.4	5.8
Mean length	10.0	12.1	13.8	15.1	16.2	17.1	17.7	18.3	18.7	19.1	19.4
Mean weight	60	105	156	206	253	295	332	364	391	413	432

Note that the length increment between age three and four fish is 2.1 and that the length increments decrease for subsequent years. The standard deviation of the distribution of the lengths of the fish in each age class around the mean length at age is 2.0. Hasselblad (1966) showed that if the difference between the means of two normal distributions divided by the sum of their standard deviations is less than 1, then there is no mode corresponding to each age class. In the present case the difference between the means divided by the sum of the standard deviations is about 0.5 so that the parameters have been chosen to produce length data that are not highly informative.

The unfished equilibrium biomass level is approximately 110 000. The optimal biomass level is approximately 44 000 which is 40% of the unfished equilibrium biomass level. The maximum recruitment occurs at a biomass of about 73 000.

Sixty years of fisheries management were simulated for all the scenarios considered. For the first set of simulations all fisheries were originally virgin fisheries. The first 10 yr were patterned after a new fishery with the fishing mortality slowly increasing each year. This situation produces the best experimental design for obtaining good parameter estimates. Also, we were able to assume that the population was initially near its unfished equilibrium level which reduces by one the number of parameters which need to be estimated.

For the LH model the assumption that the population biomass is initially at its unfished equilibrium level is equivalent to setting α equal to 1 for that model. For the FD model the assumption that the population biomass is initially at its unfished equilibrium level is equivalent to setting $\alpha_{FD} = 1/(1-l)$ (equation 2.33).

The instantaneous fishing mortality rates for the first 10 yr in the first set of simulations are given below.

Year	1	2	3	4	5	6	7	8	9	10
Mortality	0.012	0.024	0.036	0.048	0.060	0.072	0.084	0.096	0.108	0.120

The models were not used to set fishing policy for years 1–10, but data from the fishery were collected for each year. The models were used to determine fishing policy from year 11–60. The policy employed was to increase or decrease the quota from each year to the next depending on whether the estimate of the biomass for next year was greater than or less than the estimate at that time of the optimal biomass level.

More precisely, suppose that at the last iteration of the simulation procedure Y years of data were simulated. Let B^{opt} denote the present estimate of the optimal biomass and let B^{proj} be the projected biomass estimate in year $Y+1$. Let D be the difference between them

$$D = B^{proj} - \hat{B}^{opt}$$

Then Q_{Y+1} the quota in year $Y+1$ is computed by

$$Q_{Y+1} = \min\{\max\{0.8\,C_Y, C_Y + 0.5\,D\}, 1.3C_Y\}.$$

Under this policy $0.8C_Y \leq Q_{Y+1} \leq 1.3C_Y$. This policy reflects the difficulties in making large changes in quotas from one year to the next, especially the unpopularity of large decreases in quotas. The quota is not implemented directly in that C_{Y+1} is not

set equal to Q_{Y+1}. This is done for technical reasons. If the model sets $Q_{Y+1} > B_{Y+1}$ so that the quota is larger than the population, obviously the catch must be smaller than the quota. The quota is implemented by setting the level of effective effort E_{Y+1} according to the relationship

$$E_{Y+1} = \frac{Q_{Y+1}}{C_Y} E_Y.$$

Note that this is not management by effort allocation. The effective effort E_Y is an internal model parameter which serves to produce a catch C_{Y+1} which is generally close to Q_{Y+1}. Using equations 1.2 and 1.3 or equivalently 2.8 and 2.9 it follows that

$$C_{Y+1} = (1 - (1 - C_Y/B_Y)^{Q_{Y+1}/C_Y})B_{Y+1},$$

an expression in which the effective effort E_{Y+1} does not explicitly appear.

Grouping for the different time series of fisheries data.

Grouping	Catch 1	Mean Weight 5	Mean length 3	Length variance 5	Skewness 10	Kurtosis 10

The penalty weights for fitting the FD model to the length and weight data were calculated according to the method described in Fournier and Doonan (1987) which use the variance of the sampling moments, skewness, and kurtosis for a normal distribution from Kendall and Stuart (1958).

Statistic	Variance
M_i^{obs}	M_{i2}/n_i
μ_{i1}^{obs}	μ_{i2}/n_i
μ_{i2}^{obs}	$2(\mu_{i2})^2/n_i$
κ_{i3}^{obs}	$6/n_i$
κ_{i4}^{obs}	$24/n_i$

The quantities M_{i2} and μ_{i2} are not known. They have been approximated by using their estimated values M_{i2}^{obs} and μ_{i2}^{obs}. The penalty weights should be set equal to the inverse of the variances so that using this scheme the penalty weight for κ_{i3} would be equal to 400/6 or 66.7 while the penalty weight for κ_{i4} would be equal to 400/24 or 16.7. The scheme used to determine the penalty weights is admittedly rather arbitrary. We don't feel, however, that the results obtained are very sensitive to the specific values of the penalty weights chosen for the skewness and kurtosis. To test this sensitivity we have used values for the penalty weights p_5 and p_6 in the simulations which are both larger (2000 and 500) and smaller (0 and 0) than these quantities.

These penalty weights were used for the grouped data even though grouping reduces the standard deviation of the deviation of the random errors of the grouped data. This reflects our preference for the conservative use of the higher length moment data in the model.

The size of the penalty weight p_1 was based on the assumption that the variance, σ_ϵ^2, of the random component of the relationship between observed and effective effort is 0.36. The size of the penalty weight p_2 was based on the assumption that the variance, σ_η^2, of the random component of the stock–recruitment relationship is 0.16. The size of the penalty weight p_0 was based on the assumption that the variance, σ_δ^2, of the random error in the estimation of the logarithm of the catches is 0.01.

For the FD–LH model the penalty weights were the same as for the FD model. The extra penalty weight p_8 (equation 3.2) was set equal to 1.0.

In order to have an absolute measure of performance the simulations were also performed for the situation where the optimal biomass B^{opt} and the biomass in the next period B_{i+1} were known without error. This is referred to as the PI model. The results from the PI model represent the best possible performance which can be obtained under the policy chosen.

For each set of simulation runs two measures of performance were compiled. While a simple model of the type used in this paper might adequately represent a fish population over a moderate range of exploitation, experience with real fisheries has shown that as the exploitation rate increases the fish population is more likely to experience a catastrophic collapse. With this fact in mind we have recorded the minimum biomass level for the fish population for each simulation. As a general measure of performance we have tabulated the total catch for each simulation over the 60-yr period.

Although the LH model has the highest average minimum biomass level, it exhibits less stability than either the FD model or the FD–LH model. Note that four of the minimum biomass levels for the LH model are lower than the smallest minimum biomass level achieved for the FD–LH model.

TABLE 1. Values of the penalty weights used for fitting the models.

Model component	Catch Dev's p_0	Effort Dev's p_1	Recruitment Dev's p_2	Mean weight p_7	Mean length p_8	Length variance p_4	Skewness p_5	Kurtosis p_6
LH Model (equation 1.9)								
Weight	50.0	1.4						
FD Model (equation 2.14)								
Weight	50.0	1.4	3.1	1.0	62.0	5.0	2000	500
FD2 Model (equation 2.14)								
Weight	50.0	1.4	3.1	1.0	62.0	5.0	0.0	0.0

TABLE 2. Minimum biomass levels over 60 yr for good experimental design.

Simulation	LH	FD	FD–LH
1	26 430	12 590	22 100
2	8 094	23 290	20 760
3	24 970	29 700	22 500
4	13 620	17 600	16 240
5	28 860	18 460	25 920
6	37 740	21 050	29 360
7	15 710	24 510	17 780
8	31 660	14 440	18 940
9	23 860	23 200	29 400
10	14 230	23 410	21 580
Average over 10 simulations	22 517	20 825	22 458

There is very little difference between the performance of the three models in terms of the total catch for the good experimental design. The decision whether to use the more complicated FD–LH model in this situation must rest on how seriously the manager views the superior performance of the FD–LH model in terms of the minimum biomass level to which the population is driven when managed by the two models.

For the second set of simulations 80 yr of data were simulated. The fishery was heavily exploited for 20 yr before any data were gathered. The instantaneous fishing mortality rate during this period was 0.36. This resulted in the initial biomass of 110 000 being reduced to between 38 000 and 55 000 which is between 35 and 50% of its initial unfished level before any data were gathered. (The large amount of variability in the reduction of the biomass is due to the large random component in the stock–recruitment relationship). This exploitation history produces an experimental design which contains much less information for estimating the parameters than that obtained when starting with the unfished population. After the initial 20-yr period, data were then gathered for 10 yr but not used for policy formulation. During this period the instantaneous fishing mortality was also set equal to 0.36. The model was used for policy formulation for years 31 to 80.

Adaptive simulation can also be used to investigate technical

TABLE 3. Total catches over 60 yr for good experimental design.

Simulation	LH	FD	FD–LH	PI
1	539 570	535 820	578 470	602 200
2	536 910	620 190	622 690	646 860
3	474 550	560 460	601 700	635 930
4	530 340	496 650	490 600	551 220
5	635 050	572 910	600 870	635 930
6	590 330	614 270	617 740	630 190
7	721 800	723 590	721 640	770 840
8	644 930	546 630	578 760	660 110
9	642 940	613 990	619 200	647 300
10	486 480	499 610	492 990	526 410
Average over 10 simulations	580 290	578 410	592 460	630 690
Fraction of average for the PI model	0.920	0.917	0.940	1.000

TABLE 4. Minimum biomass levels over 60 yr for bad experimental design.

Simulation	LH	FD	FD2	FD–LH	FD–LH2
1	4 127	3 292	18 440	25 880	18 740
2	2 873	11 760	8 201	16 570	23 930
3	3 310	17 410	1 795	17 410	22 640
4	15 390	11 430	10 080	15 860	15 790
5	3 278	12 670	22 640	21 700	8 377
6	13 970	8 067	6 890	16 230	17 940
7	3 725	9 946	19 860	16 070	14 610
8	7 348	9 596	24 300	10 560	24 300
9	26 170	19 860	11 310	23 350	27 680
10	19 040	21 950	11 130	20 270	17 760
Average over 10 simulations	9 923	12 598	13 464	18 390	19 176

TABLE 5. Total catches over 60 yr for bad experimental design.

Simulation	LH	FD	FD2	FD–LH	FD–LH2	PI
1	416 000	299 000	534 000	578 000	545 000	560 000
2	455 000	444 000	350 000	557 000	573 000	629 000
3	406 000	551 000	328 000	543 000	555 000	597 000
4	481 000	434 000	337 000	525 000	484 000	568 000
5	403 000	537 000	576 000	574 000	507 000	597 000
6	522 000	441 000	373 000	565 000	563 000	625 000
7	545 000	586 000	6575 000	663 000	689 000	746 000
8	459 000	486 000	518 000	523 000	592 000	631 000
9	560 000	598 000	543 000	569 000	576 000	657 000
10	585 000	471 000	536 000	623 000	595 000	708 000
Average over 10 simulations	483 000	484 000	477 000	572 000	568 000	632 000
Fraction of average for the PI model	0.76	0.77	0.75	0.91	0.90	1.00

questions about model design. For example, it is possible that the higher length moments (in the form of skewness and kurtosis) contain essentially no information which is not already contained in the catch, mean weight, and lower length moment data time series. If this is so it is an important fact since the omission of the skewness and kurtosis data results in a simpler and probably more robust model. To investigate whether the inclusion of the skewness and kurtosis data result in improved model performance, the second set of simulations were performed for the model both with and without the inclusion of the skewness and kurtosis time series. The FD and FD–LH models without fitting the skewness and kurtosis data are referred to as the FD2 and FD–LH2 models. For the FD–LH2 model the penalty weights were the same as for the FD2 model (see Table 1). The extra penalty weight p_8 (equation 3.2) was set equal to 1.0, the same as for the FD–LH model.

The minimum biomass levels are considerably lower for the bad experimental design than with the good experimental design for both the LH and FD models. The performance of the LH model has degraded the most. For five of the ten simulated runs it appears that the population could have been driven to extinction. (Recall that the unfished equilibrium biomass level is about 110 000 while the biomass level which produces the maximum yield is about 44 000 so that a biomass level of 4127 is approximately 3.6% of the unfished equilibrium biomass level and approximately 9.1% of the biomass level which produces the maximum yield.)

The FD model is considerably more stable than the LH model and perhaps slightly more stable than the FD2 model. The difference between the FD and FD2 models is so small that it would require considerably more simulations to distinguish between them. The FD–LH model is clearly more stable than either the LH model or the FD model for this set of simulations. The difference in stability between the FD–LH mode and the FD–LH2 model is very slight.

For the bad experimental design the composite FD–LH model performs considerably better than either the LH model or the FD model. There is very little difference between the FD–LH model and the FD–LH2 model. The LH model works about as well as the FD model for both sets of simulations with respect to the total catch criterion. The LH model appears to be inferior to the FD model with respect to the minimum biomass level criterion. The FD–LH model is the best performer in both sets of simulations. There seems to be a synergistic effect obtained by combining the two models. These composite models deserve further study.

Simulation results of this type could be used as a basis for a cost benefit analysis. For example if it is determined that the fishery is to be managed by catch and effort data alone, then the cost of not collecting data for the first 20 yr of the fishery is a reduction in the relative performance of the management scheme from 92 to 76%, that is between 15 and 20%. In a fishery with an average value of about 1 million dollars a year this represents a cost of about 180 000 dollars.

For the same fishery the value of gathering length data in addition to gathering catch and effort data when starting a management scheme after 20 yr of exploitation is about 180 000 dollars a year.

There is no reason to believe that the type of results we have obtained for the combination of the length-based FD model and the biomass dynamic based LH model are unique to those two models. It would be interesting to carry out similar simulation studies with a catch-at-age model such as Fournier and Archibald (1982) combined with a biomass dynamic based model such as the LH model or the Schaeffer model (Schaeffer 1954). It would also be interesting to extend these studies to situations where the catchability is not stationary, for example when there is a time-dependent trend in catchability, or when the catchability has a biomass-dependent component.

Finally, we note that the results reported here are in no way exhaustive. There is no limit to the different kinds of fish population and fisheries which can be simulated in this type of analysis. We hope we have indicated how a potential model user can carry out his or her own simulation analysis for a fish population of interest and that this paper will stimulate investigation into the use of composite models for fisheries management.

Acknowledgments

We are grateful to Don Ludwig and Carl Walters for advice concerning the adaptive control of fisheries. Chris Francis and Jon Schnute reviewed the manuscript and made many helpful comments. The first author was partially supported by Natural Sciences and Engineering Research Council operating grants A-9544 and A-9239.

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Use of Lake Fossil Diatom Assemblages to Determine Historical Changes in Trophic Status

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Agbeti, M., and M. Dickman. 1989. Use of lake fossil diatom assemblages to determine historical changes in trophic status. Can. J. Fish. Aquat. Sci. 46: 1013–1021.

Based on the composition of surface sediment diatom assemblages of 30 lakes a classification index for lake trophic status was developed. The lakes were selected to represent a continuum ranging from oligotrophic to eutrophic lake types. A trophic index quotient was derived. The log diatom inferred trophic index (D.I.T.I.) was regressed against the trophic status of the lakes as determined by the log total phosphorus ($r=0.84$) and log chlorophyll-a ($r=0.91$). Multiple regression analyses showed significant correlations between log D.I.T.I. and the log percentage abundances of oligotrophic, mesotrophic, and eutrophic species ($r=0.89$). The abundance of the trophic indicator diatom species depends not only on total phosphorus and chlorophyll-*a*, but possibly on the interaction of these with other factors. Using this approach, past trophic changes were inferred for oligotrophic Barbara Lake and eutrophic Chemung Lake. The study suggested that Barbara Lake had retained its present day oligotrophic condition over the last 200 yr, whereas major trophic changes have occurred in Chemung Lake.

On a établi un indice de classification de l'état trophique des lacs d'après la composition des assemblages de diatomées dans les sédiments superficiels. Les lacs ont été sélectionnés de façon à ce que tous les types lacustres soient représentés, depuis le milieu oligotrophe jusqu'au plan d'eau eutrophe. On a déterminé un quotient de l'indice trophique. On a effectué la régression de la courbe logarithmique de l'indice trophique obtenu à partir des diatomées, en fonction de l'état trophique des lacs déterminé par la courbe logarithmique du phosphore total ($r=0,84$) et celle de la chlorophylle a ($r=0,91$). Les analyses de régression multiple ont montré des corrélations significatives entre la courbe logarithmique de l'indice trophique et celle de l'abondance en pourcentage des espèces oligotrophes, mésotrophes et eutrophes ($r=0,89$). L'abondance des espèces de diatomées indicatrices de l'état trophique dépend non seulement du phosphore total et de la chlorophylle a, mais aussi, peut-être, de l'interaction de ces composantes avec d'autres facteurs. On a utilisé cette approche pour expliquer l'apparition de changements trophiques antérieurs dans le lac Barbara qui est oligotrophe et le lac Chemung qui est eutrophe. Les résultats de l'étude indiquent que le lac Barbara est oligotrophe depuis 200 ans, tandis que des changements trophiques importants ont eu lieu dans le lac Chemung.

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Diatoms have been widely used as indicators of lake trophic status and lake productivity (Stockner and Benson 1967; Stockner 1971; Battarbee 1978; Bradbury 1988; Brugam 1988). Nygaard (1956) proposed a C:P (Centrales:Pennales) ratio which he correlated with lake productivity. The ratio was based on the fact that oligotrophic lakes contain many Monoraphidineae and Biraphidineae spp. which originate in the epiphytic, epipelic, and epilithic communities of these lakes rather than on trophic status per se. The C:P ratio becomes unrealistically high in very large lakes containing large amounts of suspended materials (Stockner and Benson 1967). Moreover, the presence of several centric diatoms in eutrophic lakes gives high values of the index (Stockner and Benson 1967).

Stockner's (1971) A:C (Araphidineae:Centriceae) index has been applied to document the level of lake eutrophication (Bailey and Davis 1978; Brugam 1978; Culver et al. 1981; Stockner 1972, 1975). However, the ratio is not particularly useful in assessing the trophic status of shallow lakes and bogs (Stockner 1972) where benthic diatoms or heavily silicified centric diatoms often predominate independent of the trophic status of the waterbody. Stockner (1972) also recognized that the ratio may not be applicable to lakes that have remained mesoeutrophic throughout most of their postglacial history (e.g. prairie lakes). A high A:C ratio, typical of eutrophic conditions, is characteristic only of moderate phosphorus loadings and low alkalinities (Brugam and Patterson 1983; Wetzel 1983). In order to develop a better diatom inferred trophic index, we examined whether total phosphorus and chlorophyll-*a*, used as independent measures of trophic status, can be correlated with the ratio of eutrophic to oligotrophic diatom assemblages.

Thirty lakes were selected for this study, representing a broad cross-section of lakes from Ontario (Wawa, Sudbury, Peterborough, and Haliburton regions), Quebec, and Nova Scotia (Kejimkujik National Park). The lakes represent a continuum from oligotrophic to eutrophic conditions. The trophic index developed here would be applicable to diverse lake types.

Materials and Methods

Sediment cores were collected from the profundal zones of each of the 30 study lakes using a K-B gravity corer (Brinkhurst et al. 1969). The cores were sectioned in intervals of 2 mm to

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TABLE 1. Location and mean annual epilimnetic concentrations of total phosphorus (TP) and chlorophyll *a* (Chla) of 30 study lakes.

Lake	TP ($mg \cdot m^{-3}$)	Chl-*a*	Location		Source of TP and Chl-*a*
			Town/region	Long. and Lat.	
1. Frederick	2.0	0.3	Sudbury	47°02′N, 81°00′W	Pitbaldo, Laurentian University[d]
2. Majorie	5.0	0.4	"	"	"
3. Dougherty	3.0	0.1	"	"	"
4. Bluesucker	9.0	0.5	"	"	"
5. Pilgrim	7.0	0.6	"	"	"
6. Chiniguchi	3.0	0.1	"	"	"
7. Matagamasi	8.0	0.7	"	"	"
8. Silvester	2.0	0.2	"	"	"
9. Big Dam West	11.1	1.7	Nova Scotia	44°29′N, 65°27′W	Kerekes (1975)
10. Big Dam East	7.9	1.2	"	"	"
11. Beaverskin	4.7	1.4	"	"	"
12. Kejimkujik	9.1	2.1	"	"	"
13. Pebbleloggitch	10.0	1.6	"	"	"
14. B-Wawa	6.5	1.9[a]	Algoma	48°20′N, 86°05′W	Dickman and Thode (1985)
15. Doc Grieg	9.0[a]	1.5	"	"	"
16. Crozier	10.5[a]	2.1	"	"	"
17. Kenessis	10.6[a]	1.9	Haliburton	45°13′N, 78°30′W	OME (1986)
18. 12-Mile	14.3[a]	1.8	Haliburton	45°13′N, 78°30′W	OME (1986)
19. Stony	17.0	4.3	Kawartha	44°20′N, 78°30′W	OME and MNR (1976)
20. Crawford	16.5	3.9	North of Hamilton	43°28′N, 79°57′W	Dickman (1985)
21. Two-Mts.	63.0	12.6[a]	Montreal	46°19′N, 73°52′W	Vincent and Bergeron (1983)
22. Upper Buckhorn	24.5	8.8	Kawartha	44°20′N, 78°52′W	OME and MNR (1976)
23. Lower Buckhorn	25.0	6.0	"	"	"
24. Chemung	26.0	7.2	"	"	"
25. Pigeon	27.0	4.3	"	"	"
26. Rice	52.5	13.8	"	"	"
27. Scugog	42.5	14.4	"	"	"
28. Julian	19.0	4.5[a]	Mt. Julian	45°05′N, 78°55′W	Sampled[e]
29. Cataraqui Marsh	17.5	4.0[a]	Cataraqui	44°14′N, 76°28′W	Sampled[e]
30. Simcoe[b]	33.0	8.8[a]	Southern Ontario	44°10′N, 79°30′W	OME and MNR (1985)
31. Barbara[c]	2.7	0.8	Algoma	48°20′N, 86°05′W	Pitbaldo, Laurentian University[d]

[a]Estimated from a regression curve of total phosphorus versus chlorophyll-*a*.
[b]Excluded from the regression analysis used to construct the curves in Fig. 2 and 3.
[c]Used for downcore profile analysis only.
[d]Data supplied to Pitbaldo, Geography Department, Laurentian University, Sudbury, Ontario by Ontario Ministry of the Environment.
[e]Sampled = value taken at the same time of sampling for diatom analysis.

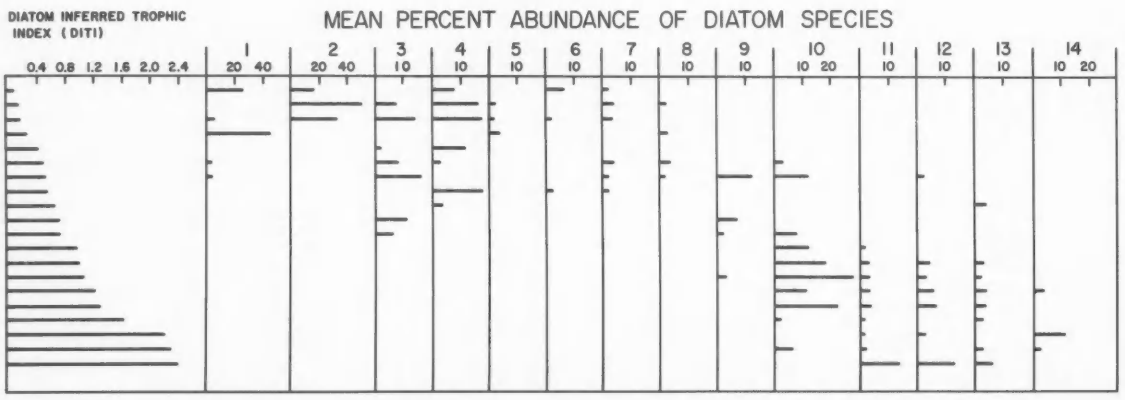

FIG. 1. Mean percentage abundance of the common diatom species in relation to the diatom inferred trophic index (D.I.T.I.). Numbers at the top of the graphs indicate the species used. 1 = *Fragilaria acidibiontica*; 2. = *F. constricta*; 3 = *Cyclotella comta*; 4, = *Melosira lirata*; 5 = *M. lirata* var. *lacustris*; 6 = *M. lirata* var. *biseriata*; 7 = *M. perglabra* var. *flourinae*; 8 = *M. distans*; 9 = *F. crotonensis*; 10 = *F. construens*; 11 = *F. pinnata*; 12 = *M. ambigua*; 13 = *M. granulata*; 14 = *Stephanodiscus astraea*.

TABLE 2. Dominant species found in each of the lake types. The letters against each of the species indicate the trophic status indicator as obtained from the literature (0 = oligotrophic indicator; M = mesotrophic indicator; E = eutrophic indicator; ND = no data).

Dominant species in oligotrophic lakes
Anomeoneis serians (O)
Cyclotella comta(O)
Fragilaria acidobiontica (O)
F. constricta (O)
Pinnularia maior (O)
P. viridis (O)
P. stomatophora (O)
Eunotia pectinalis (O)
E. pectinalis var. *ventricosa* (O)
E. serra (O)
E. gibbosa (O)
Melosira distans (O)
M. lirata var. *lacustris* (ND)
M. lirata var. *biseriata* (ND)
M. perglabra (ND)
M. cf. *goetzeana* (ND)
Dominant species in mesotrophic lakes
Fragilaria crotonensis (M)
F. construens (M)
Cyclotella comta (O)
C. glomerata (O)
C. meneghiniana (M)
Dominant species in eutrophic lakes
Stephanodiscus astraea (E)
S. niagarae (E)
Melosira ambigua (E)
Fragilaria pinnata (E)
F. brevistriata (E)
Achnanthes lanceolata var. *rostrata* (*E*)

TABLE 3. Literature-derived trophic status, diatom inferred trophic index, and diatom inferred trophic status of the 30 study lakes. The lake numbers used in this table correspond to numbers marked in Fig. 2 and 3.

Lake	Literature-derived trophic status[a]	D.I.T.I. value	Diatom-inferred trophic status[b]
1. Frederick	U-OL	0.06	OL
2. Majorie	U-OL	0.03	OL
3. Dougherty	OL	0.13	OL
4. Bluesucker	OL	0.06	OL
5. Pilgrim	OL	0.05	OL
6. Chiniguchi	U-OL	0.12	OL
7. Matagamasi	OL	0.15	OL
8. Silvester	U-OL	0.15	OL
9. Big Dam West	OL	0.64	OL
10. Big Dam East	OL	0.35	OL
11. Beaverskin	OL	0.63	OL
12. Kejimkujik	OL	0.66	OL
13. Pebbleloggitch	OL	0.69	OL
14. B-Wawa	OL	0.26	OL
15. Doc Crieg	OL	0.49	OL
16. Crozier	OL	0.40	OL
17. Kennesis	OL	0.44	OL
18. 12-Mile	O-M	0.51	OL
19. Stony	M	0.97	M
20. Crawford	M	0.90	M
21. Two-Mts.	E	2.23	E
22. Upper Buckhorn	M-E	2.43	E
23. Lower Buckhorn	M-E	2.27	E
24. Chemung	M-E	1.22	M
25. Pigeon	M-E	1.62	M
26. Rice	E	1.70	E
27. Scugog	E	1.28	E
28. Julian	M	1.62	E
29. Cataraqui	M	1.15	M
30. Simcoe[c]	E	14.10	

[a]For the designation of the literature-derived trophic status, see materials and methods section and Table 1 (U-OL = ultraoligotrophic; OL = oligotrophic; M = mesotrophic; M-E = mesoeutrophic; E = eutrophic).

[b]Diatom inferred trophic status was based on the frequency distribution pattern of D.I.T.I. values (Fig. 4).

[c]Excluded from the linear regression analyses because of the unrealistically high D.I.T.I. value in comparison to the other lakes.

2 cm with the thickest sections being taken near the base of the cores.

The diatoms were recovered from the sediments using the hydrogen peroxide method (Kingston 1986) and slides were prepared by Battarbee's (1973) technique. Six hundred diatom frustules were counted for each sample under oil immersion (1000 ×). The data for each of the species were expressed in terms of their relative abundances. Diatom identifications were based on Cleve-Euler (1951–1955); Hustedt (1930, 1939); Patrick and Reimer (1966, 1975); Gerloff and Cholnoky (1970); Bourrelly (1981); Germain (1981); Nichols (1983); and Camburn et al. (1984–1986).

Diatoms were assigned a trophic indicator status based on autecological descriptions provided by Hustedt (1930, 1939); Patrick and Reimer (1966, 1975); Gerloff and Cholnoky (1970); and the data compiled by Beaver (1981). The diatom species were divided into six groups: (1) oligotrophic indicators; (2) oligomesotrophic indicators; (3) mesotrophic indicators; (4) mesoeutrophic indicators; (5) eutrophic indicators; and (6) eurytypic species and species with little or no trophic status data available.

Multiple regression analysis was performed to determine the correlation between the trophic status (as determined by each of log transformed total phosphorus and chlorophyll-*a*) and each of the following: (1) log transformed percentage abundances of oligotrophic, mesotrophic, and eutrophic species; (2) the log transformed percentage abundances of 20 dominant species. To find the best combination of the diatom groups to determine the trophic index, the groups were treated in four ways to develop four different ratios:

(i) D.I.T.I. = eut/oligo
(ii) D.I.T.I. = eut + meso-eut/oligo + oligo-meso
(iii) D.I.T.I. = eut + meso/oligo + meso
(iv) D.I.T.I. = eut + meso + meso-eut + oligo-meso/ oligo + meso + meso-eut + oligo-meso,

where eut = the sum of eutrophic species; oligo = the sum of oligotrophic species; meso = the sum of mesotrophic species; oligo-meso = the sum of oligomesotrophic species, and meso-eut = the sum of mesoeutrophic species. In all cases eurytypic species and species with no trophic status data were excluded from the equation. The ratios (indices) derived from each of these treatments were regressed against the total phosphorus

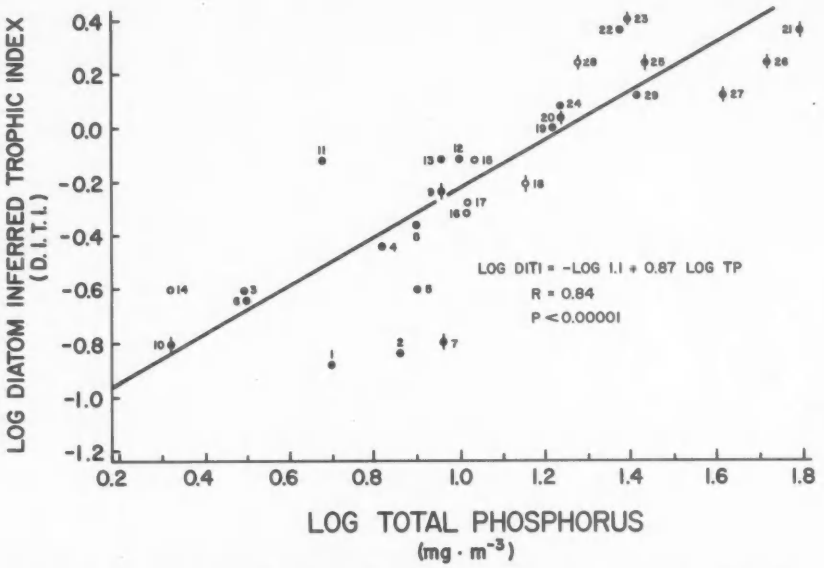

FIG. 2. Relationship between log diatom inferred trophic index (D.I.T.I.) and log total phosphorus ($r=0.84$; $n=29$, $p<0.00001$). (●) Data points available in the literature. (○) Data points estimated from the regression curve of total phosphorus and chlorophyll-*a*. Vertical and horizontal bars above and below the plotted points represent the ranges based on two counts from randomly selected slides.

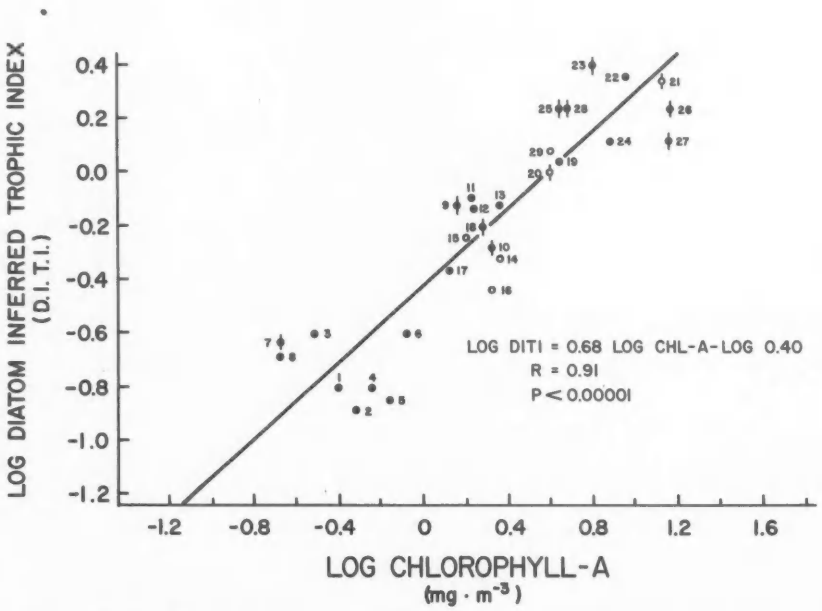

FIG. 3. Relationship between log diatom inferred trophic index (D.I.T.I.) and log chlorophyll-*a* ($r=0.91$; $n=29$; $p<0.00001$). (●) Data points available in the literature. (○) Data points estimated from a regression curve of total phosphorus versus chlorophyll-*a*. Vertical and horizontal bars above and below the plotted points represent ranges based on two counts from randomly selected slides.

TABLE 4. Equations for the linear regression (log D.I.T.I. against each of log total phosphorus and chlorophyll-*a*) and the multiple regressions of each of log total phosphorus, log chlorophyll-*a*, and log D.I.T.I. against log abundances of oligotrophic, mesotrophic, and eutrophic species and 20 dominant species.

Linear regressions

(1) Log D.I.T.I. = 0.68 log chl-*a* − log 0.40
$r = 0.91$; $n = 29$; SE = ±0.17; $p < 0.00001$.
(2) Log D.I.T.I. = 0.87log TP − log 1.1
$r = 0.84$; $n = 29$; SE = ±0.22; $p < 0.00001$.

Multiple regressions

(1) Log total phosphorus and the log percentage abundances of oligotrophic, mesotrophic, and eutrophic species.
log TP = log 0.84 − 0.13 logol + 0.31 logme + 0.12 logeu[a]
$r = 0.85$; $n = 29$; SE = ±0.12; $p < 0.00001$.
(2) Log total phosphorus and the log percentage abundances of 20 dominant species.
Log TP = log 1.08 + 0.27 *F. construens*
$r = 0.78$; $n = 29$; SE = ±0.24; $p < 0.00001$.
(3) Log chlorophyll-*a* and the log percentage abundances of oligotrophic, mesotrophic, and eutrophic species.
log chl-*a* = −log 0.15 − 0.15 logol + 0.55 logme + 0.16 logeu.
$r = 0.87$; $n = 29$; SE = ±0.27; $p < 0.00001$.
(4) log chlorophyll-*a* and the log percentage abundances of 20 dominant species.
log chl-*a* = log 0.57 + 0.37 log *F. construens* + 0.35 log *E. pectin* − 0.14 *F. acidobionitica*.
$r = 0.85$; $n = 29$; SE = ±0.29; $p < 0.00001$.
(5) Log D.I.T.I. and the log percentage abundances of oligotrophic, mesotrophic, and eutrophic species.
log D.I.T.I. = −log 0.33 − 0.17 logol + 0.27 logme + 0.13 logeu.
$r = 0.89$; $n = 29$; SE = ±0.20; $p < 0.00001$.
(6) Log D.I.T.I. and the percentage abundances of 20 dominant species.
log D.I.T.I. = −log 0.23 + 0.19 log *F. construens* − 0.17
log *F. constricta* − 0.11 log *F. acidobionitica* − 0.11 log *C. comta* + 0.17 log *A. serians*.
$r = 0.89$; $n = 29$; SE = ±0.19; $p < 0.00001$.

[a]Logol = log oligotrophic species; logme = log mesotrophic species; logeu = log eutrophic species.

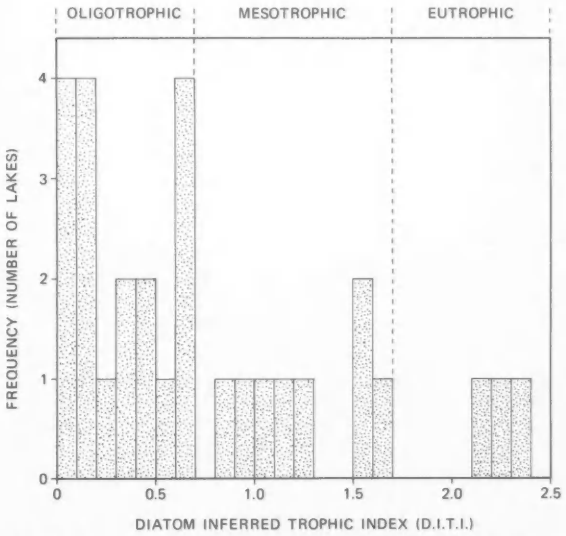

FIG. 4. Frequency distribution pattern (histogram) of the diatom inferred trophic indices (D.I.T.I.) values for 29 of the study lakes (that is, excluding Lake Simcoe). This figure was used to determine the split points for diatom inferred trophic status.

and chlorophyll-*a* for the 30 lakes in order to determine the best fit.

The best fit diatom inferred trophic indices (D.I.T.I.'s) obtained from the surface sediments of each of the 30 lakes were used to develop regression curves of log D.I.T.I. versus the log of the mean annual concentrations of total phosphorus and chlorophyll-*a* for each of the 30 lakes. Multiple regression analyses were also performed to determine the correlation between log D.I.T.I. and each of (1) the log percentage abundances of oligotrophic, mesotrophic, and eutrophic species and; (2) 20 dominant species.

Data for the total phosphorus and chlorophyll-*a* were obtained from the Ministry of the Environment and other publications (Table 1), but were not always available for all lakes. A regression curve of total phosphorus versus chlorophyll-*a* was used to estimate the missing values. All values derived in this manner are designated with an "o" mark in the figures.

Results

Each of the lake trophic types was dominated by distinct diatom assemblages (Table 2). *Melosira* cf. *goetzeana* occurred in exceptionally high numbers in the humic Big Dam East, Big Dam West, and Pebbleloggitch lakes. These dystrophic lakes have higher productivity in comparison to typical oligotrophic lakes (Kerekes 1975). Eutrophic indicator species occurred in low numbers in the mesotrophic lakes and a few mesotrophic

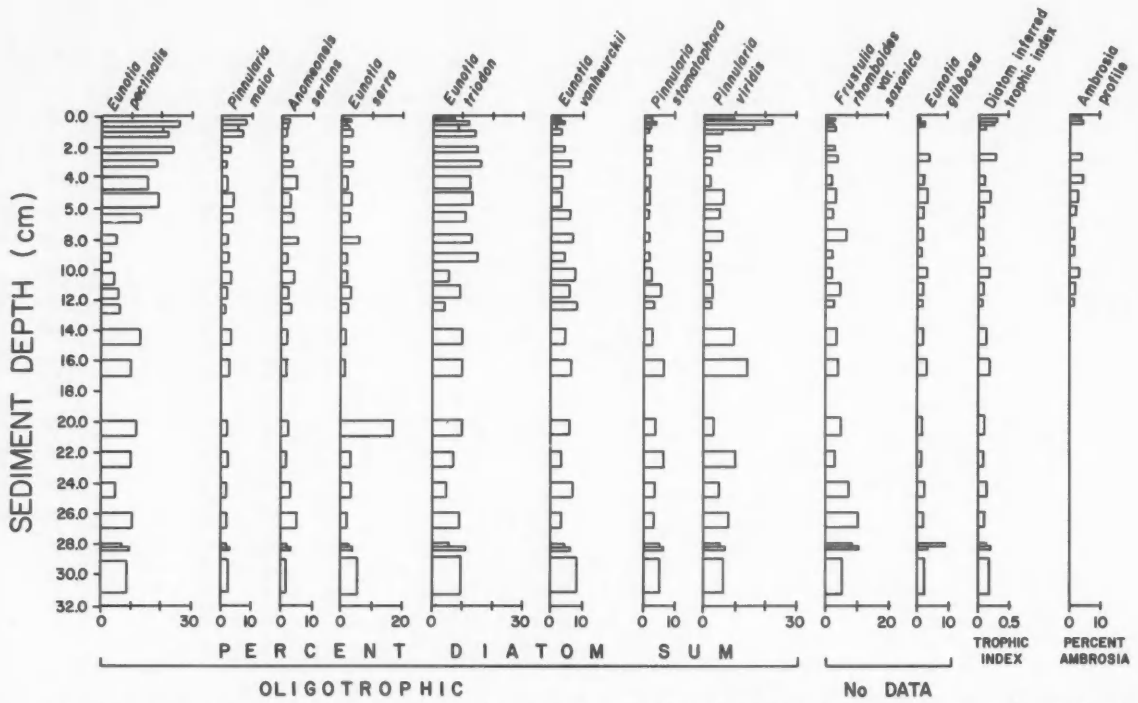

FIG. 5. Downcore profile of the common diatom species, diatom inferred trophic index (D.I.T.I.) and *Ambrosia* rise for Barbara Lake. The horizontal bars at 0.5, 7.0, 16.5, 29.5, and 31.5 cm represent ranges for replicated ($n = 2$) diatom counts at these depths. "No data" represent species with insufficient or no data available on their trophic status.

species were consistently present in eutrophic lake types. The number of the dominant taxa in each lake decreased as the inferred index increased (Fig. 1).

With the exception of Lake Simcoe, the inferred index for the lakes ranged from 0.03 to 2.43 (Table 3). In Lake Simcoe 80% of the total diatom population was a single species (*Stephanodiscus astraea*). As a result, the inferred index of this lake was unrealistically high compared with the other lakes (Table 3). When Lake Simcoe was included in the regression of the inferred indices with total phosphorus and chlorophyll-*a*, correlation coefficients of 0.31 and 0.26 were obtained, respectively. Its exclusion from the regression greatly improved the correlation coefficients (Fig. 2 and 3).

The data for the literature-derived trophic status, the diatom inferred trophic index, and the diatom inferred trophic status are presented in Table 3. Among the four treatments performed (i) to (iii) gave r values ranging from 0.31 to 0.54 when the index used in deriving each of them was regressed with total phosphorus and chlorophyll-*a*. The index derived from treatment (iv) showed high correlations with both total phosphorus and chlorophyll-*a* (Fig. 2 and 3). Chlorophyll-*a* gave a slightly higher r value (Table 4). The multiple regression of each of the log transformed values of total phosphorus, chlorophyll-*a*, and the inferred index against each of percentage abundance of the trophic indicator groups (oligotrophic, mesotrophic, and eutrophic species) and the 20 dominant species also gave significant correlations (Table 4). When log D.I.T.I., log total phosphorus, and log chlorophyll-*a* were regressed with each of the percent abundances of the three trophic indicator groups and the 20 dominant species, D.I.T.I. gave higher r values.

Because of the high degree of overlap between oligomesotrophic to mesoeutrophic categories, it was not possible to discriminate between these mesotrophic lake types. A histogram of the D.I.T.I. values was constructed to determine the frequency groups (Fig. 4). Based on this histogram, three categories of diatom inferred trophic status were recognized: oligotrophy (D.I.T.I. = 0–0.69), mesotrophy (0.70–1.69) and eutrophy (1.70–2.50). Most of the lakes studied were in the oligotrophic group followed by the mesotrophic group and eutrophic lakes rarely were included (Fig. 4).

Discussion

The relationship between log D.I.T.I. (obtained by including the mesotrophic species) and log total phosphorus and log chlorophyll-*a* showed significant correlations (Fig. 2 and 3). In both cases more than 60% of the variation in the inferred index was explained by the trophic status parameters, total phosphorus, and chlorophyll-*a* (r^2 values of 0.66 and 0.83, respectively). The variability within the trophic status parameters might be attributed to the fact that the data were obtained from different sources that may have inherent errors. Another source of variability might be the poor correlation between total phosphorus and algal production, especially during spring and fall overturn. This may be due to limitation by temperature or light (Carlson 1977) and the reduction of the summer mean chlorophyll-*a* yield per unit phosphorus by inorganic solids (Hoyer and Jones 1983). In addition, there were some dominant diatoms, especially *Melosira* spp., for which no data on trophic status were avail-

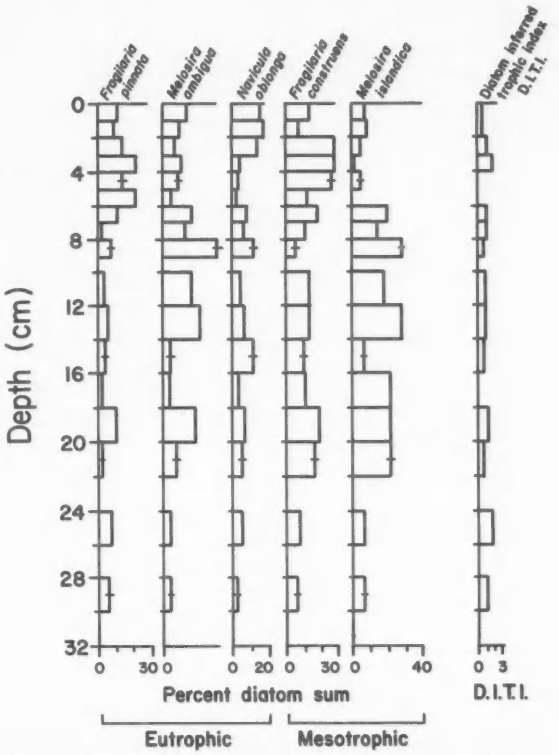

FIG. 6. Downcore profile of the common diatom species and diatom inferred trophic index (D.I.T.I.) of Chemung Lake. The horizontal bars at 4.5, 8.5, 15.0, 21.0, and 29.0 represent ranges for replicated ($n=2$) diatom counts at these depths.

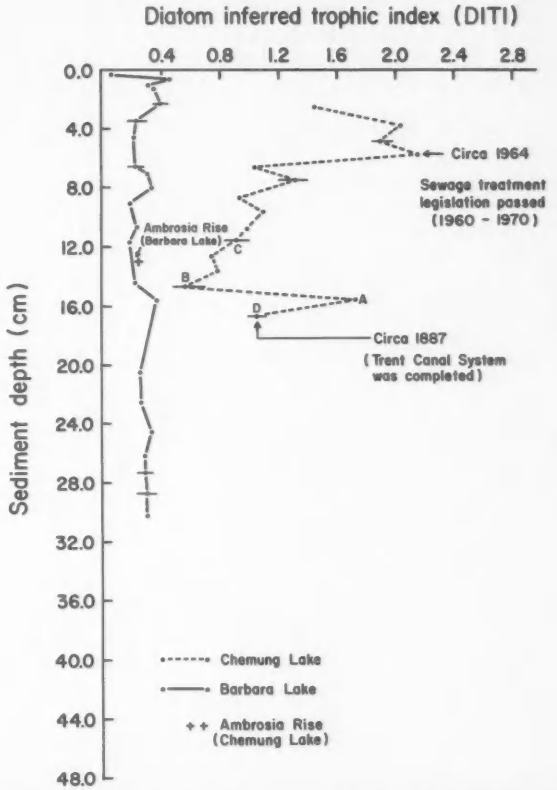

FIG. 7. Comparison of the downcore profiles of the diatom inferred trophic index (D.I.T.I.) for Barbara and Chemung Lakes. Horizontal bars represent ranges ($n=2$) diatom counts. + =The *Ambrosia* rise in Barbara Lake occurred at 12–13 cm (circa 1890; Dickman et al. 1987). + + =The *Ambrosia* rise in Chemung Lake occurred at 40–50 cm (circa 1825; Hardy 1977). A, B, and C represent depths at which high organic matter was found (Hardy 1977). D represents the depth corresponding to the year in which the Trent Canal System was completed (circa 1887; Hardy 1977).

able. Had the data on these species been available, the D.I.T.I. might have improved considerably.

Because of the unrealistically high D.I.T.I. value obtained for Lake Simcoe, it was suggested that where a diatom assemblage is dominated by only one or a few species, the D.I.T.I. technique is not applicable.

The regression of each of log total phosphorus and log chlorophyll-*a* against the log percentage abundances of oligotrophic, mesotrophic, and eutrophic species showed significant correlations (Table 4). This demonstrated the dependence of trophic status indicator species on total phosphorus and chlorophyll-*a*. Regression of log total phosphorus against the 20 dominant species showed that only one species, *Fragilaria construens* could be used to predict total phosphorus. For chlorophyll-*a*, *Fragilaria construens*, *F. acidobiontica*, and *Eunotia pectinalis* were good predictors (Table 4).

Multiple regression of log D.I.T.I. versus the 20 dominant species showed that *Fragilaria construens*, *F. constricta*, *F. acidobiontica*, *Cyclotella comta*, and *Anomeoneis serians* could be used to predict D.I.T.I. The regression of each of the 20 species individually against each of D.I.T.I., chlorophyll-*a*, and total phosphorus gave weak correlations (r values not presented). The inability of the 20 dominant species to show significant correlations with total phosphorus, chlorophyll-*a*, and the inferred index might be explained by the fact that the abundance of trophic indicator diatoms depends not only on trophic status parameters (i.e. total phosphorus and chlorophyll-*a*) but on the interaction of these variables with other factors (e.g. dissolved silica and the depths of mixed layer).

Sediment Core Profiles

There were no significant changes in the downcore inferred index in Barbara Lake (Fig. 5 and 6). Ten common species showed no significant downcore changes. All these taxa are oligotrophic species. No eutrophic species were observed in the 32-cm long core. Historically, there has been no human habitation in the lake's watershed (Fortescue et al. 1981). It is possible to suggest that Barbara Lake has remained oligotrophic over the past 200 yr.

Among the five common trophic indicator diatoms found in Chemung Lake, *Melosira ambigua*, *Fragilaria pinnata*, and *Navicula oblonga* are eutrophic and *F. construens* and *M. islandica* are mesotrophic species (Fig. 6).

The inferred index in Chemung Lake ranged between 2.2 (5–6 cm) and 0.57 (21 cm). *Melosira islandica* became very abundant in the 6–21 cm depths which corresponds to the period when the lake water level was substantially increased as a result

of the construction of the Trent Severn Canal in the 1800's (Hardy 1977). During this period, the numbers of eutrophic taxa (except *M. ambigua*) were relatively low (Fig. 6 and 7). Thereafter (2–6 cm), there was a change from the predominance of mesotrophic to eutrophic species (*Navicula oblonga* and *Fragilaria pinnata*). The change in dominance from mesotrophic to eutrophic indicator species can be attributed to increased eutrophication. This apparent change in the lake's trophic status might be due to two factors: first, nutrient rich run-off associated with the building of cottages in the lake's watershed after World War II; secondly, lake shallowing caused by the construction of the Trent Canal and accompanied by the invasion of *Myriophyllum spicatum* in the 1970's (Wile 1975) might be responsible for increased habitat for numerous epiphytic diatom taxa. During the last 10–15 yr, nutrient loading to Chemung Lake has been reduced as a result of implementation of phosphorus removal legislation by the Ontario Ministry of the Environment. The lake's return to mesotrophic conditions was indicated by the increase in the mesotrophic species in the topmost layer of the sediment core and a lower inferred index.

Conclusions

Diatoms from the surface sediments of 30 lakes ranging from oligotrophic to eutrophic conditions can be classified into three broad groups; oligotrophic, mesotrophic, and eutrophic. The trophic index derived from the diatom assemblages was significantly correlated with total phosphorus and chlorophyll-*a*. However, the index might not be applicable in lakes in which the diatom assemblage is dominated by few species. The inferred trophic index can be used to classify lakes into trophic categories. Not all the individual diatom species displayed a significant correlation with total phosphorus and chlorophyll-*a* because the abundance of some diatom species was likely to be dependent on the interactions of other variables with total phosphorus and chlorophyll-*a*. The inferred index indicated that over the past 200 yr Barbara Lake has retained its present day oligotrophic conditions whereas major trophic changes have occurred in Chemung Lake.

The study indicated that the diatom inferred trophic index can be applied to lakes in Canada. However, separate calibration curves might be required for other regions of the world. The inferred index, in combination with other predictors of trophic status such as paleopigments and autochthonous organic material, should permit paleolimnologists the opportunity to improve their ability in assessing historical changes in trophic status.

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Correction of Relative Fish Abundance Estimates from Catch Data for Variable Fishing Intensity during Lake Surveys

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Six small Newfoundland lakes were fished with gillnets over a 3–6 yr period in a manner typical of standard lake surveys where surveyors have a fixed amount of gear available, but lake size varies. Catch and effort data for brook trout (*Salvelinus fontinalis*) were examined for the purpose of selecting an appropriate measure of the relative abundance of trout. Fishing effort was not a function of lake area but fishing intensity or fishing effort per unit area varied inversely with lake area. Brook trout yield (kilograms per hectare) was positively related to fishing intensity. Catch per unit effort (kilograms) of brook trout was inversely related to fishing intensity. Methods are suggested to correct for the bias in catch data resulting from variable fishing intensity during lake surveys and improve the recognition of differences in relative fish abundance.

La pêche aux filets maillants a été pratiquée dans six petits lacs de Terre-Neuve pendant une période de 3 à 6 ans d'une manière caractéristique pour les enquêtes standards sur les lacs où les enquêteurs disposent d'une quantité donnée d'engins, mais où la taille du lac varie. Les données sur les prises et l'effort pour l'omble de fontaine (*Salvelinus fontinalis*) ont été étudiées en vue de choisir une mesure appropriée de l'abondance relative de l'omble. L'effort de pêche n'était pas fonction de la superficie du lac mais l'intensité de pêche ou l'effort de pêche par unité de surface variait inversement avec la superficie du lac. Le rendement de l'omble de fontaine (kilograms par hectare) était lié de façon positive à l'intensité de pêche. Les captures par unité d'effort (kilograms) de l'omble de fontaine était inversement liées à l'intensité de pêche. Des méthodes sont proposées afin de corriger le biais des données sur les captures résultant de l'intensité de pêche variable au cours des enquêtes sur les lacs et d'améliorer la reconnaissance des différences au niveau de l'abondance relative des poissons.

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Catch data obtained with gillnets are commonly employed to compare the relative abundance of fish among populations and to show change within populations (Ricker 1975; Hamley 1980). Catch data selected have included both yield (weight of fish captured per unit area (Rounsefell 1946; Ryder et al. 1974)) and, more commonly, catch per unit of effort (weight of fish captured per unit of fishing effort (Beggs and Gunn 1986; Kelso et al. 1986)). Catches by passive fishing gear can be influenced by behavioural differences among and within species, season of capture, and various gear characteristics. Most of this influence can be alleviated by the standardization of methods (Hamley 1980; Hamley and Howley 1985) or the adjustment of catches for varying catchability (Ryan 1984).

Catch data are also influenced by the amount of fishing effort applied per unit area of habitat. Fishing effort per unit area is termed effective fishing effort or fishing intensity (Ricker 1975). Variation in fishing intensity can result in variation in catch data as a result of stock depletion and competition among nets (Ricker 1975; Hamley 1980). However, little is known about competition among nets and the influence of variable fishing intensity on catch data from lake surveys is not well documented. Customarily, fishing intensity is not standardized during lake surveys nor is variable fishing intensity corrected for in the analysis of catch data from those surveys.

In this report we provide evidence that a bias in fishing intensity occurs during standard surveys of small lakes. With brook trout (*Salvelinus fontinalis*) catch data from surveys of six lakes, we provide an example of the variation in yield and catch per unit effort attributable to variable fishing intensity. We suggest methods for correcting catch data for variable fishing intensity during standard lake surveys.

Methods

The six study lakes (Table 1), all within the boundaries of Gros Morne National Park on the west coast of insular Newfoundland, are referred to locally as ponds. The differences in salinity and mean depth suggest likely differences in potential fish production (Ryder et al. 1974). Salinity however, was a function of varying sea salt deposition (Kerekes 1978). Candlestick Pond, pH 5.2, may be limited in its production of brook trout (Power 1980; Rodgers 1984).

Brook trout, captured in all the lakes, may be sea run in Wigwam, Half Moon, and North Narrows ponds. Other fish

TABLE 1. Selected lake characteristics and catch and effort statistics for brook trout from six lakes in Gros Morne National Park, insular Newfoundland. For additional details, see Ryan and Kerekes (1988).

	Pond Point Big Pond	Candlestick Pond	Sandy Pond	Wigwam Pond	Half Moon Pond	North Narrows Pond
Latitude	49°40′	49°38′	49°19′	49°24′	49°37′	49°37′
Longitude	57°57′	57°34′	57°59′	57°37′	57°52′	57°54′
Water area (ha)	10.2	92.5	104.0	74.9	32.9	57.5
Maximum depth (m)	1.1	16.0	21.8	34.0	11.0	17.0
Mean depth (m)	0.7	4.5	9.8	14.3	3.0	6.0
Salinity (ppm)	51.7	8.2	13.9	21.9	43.2	68.8
pH	6.8	5.2	6.4	6.8	7.6	7.9
Years of fishing effort	1975–77	1975–78	1975–79	1977–80	1975–79	1975–79
Mean annual effort (units)[a]	11.42	30.82	40.10	34.07	49.93	69.03
Mean annual intensity (units·ha^{-1})[a]	1.12	0.33	0.39	0.46	1.52	1.20
Mean annual trout yield (g·ha^{-1})	519.5	36.6	253.9	249.5	373.2	283.4
Mean annual trout catch per unit effort (g·unit^{-1})[a]	463.9	109.8	658.4	548.5	245.9	236.1

[a]A unit of effort is defined as 15 m of gillnet fished for 24 h.

species captured are arctic charr (*Salvelinus alpinus*), sea run and landlocked Atlantic salmon (*Salmo salar*), American eel (*Anguilla rostrata*), and rainbow smelt (*Osmerus mordax*).

The six lakes were fished for a 2- to 6-d period from June to October in each of three to six consecutive years from 1975 to 1980 (Ryan and Kerekes 1988). Gangs of 15 and 27 m long monofilament gillnets, stretched mesh sizes 19, 25, 38, 51, 64, 76, and 89 mm, were set overnight. The mesh size compositions of the gangs of nets and the lengths of individual nets of given mesh sizes varied from time to time and place to place, depending on net damage and the availability of replacement nets. Fishing effort varied from lake to lake and year to year. Fishing effort (units) was calculated as the number of 15-m lengths of gillnets fished for 24 h and fishing intensity was calculated as the number of units of fishing effort applied per hectare of water surface area (Ricker 1975). To select an appropriate estimator of relative abundance, the relationships of fishing effort and intensity to lake area and the relationships of fishing intensity to yield and catch per unit effort were examined by least squares regression (Sokal and Rohlf 1969).

Results

Fishing effort varied considerably within and among the study lakes (Table 1) but overall, fishing effort had not been applied in proportion to lake size (Fig. 1A). A greater number of net efforts had been applied as lake size increased among the smallest three lakes but overall, mean effort was not significantly related to lake area ($p>0.10$). The least effort had been applied in the smallest lake to avoid overfishing, but removal of that lake from the regression did not result in a significant relationship between effort and lake size ($p>0.10$).

In contrast, fishing intensity was less in the larger lakes (Fig. 1B). The relationship between mean intensity (Y) and area (X) could be described by a significant simple linear function ($Y = 1.565 - 0.012X$; $r=0.832$; $N=6$; $p<0.05$). A reciprocal transformation (Sokal and Rohlf 1969) provided a slightly better fit ($1/Y = 0.154 + 0.025\ X$; $r=0.868$; $N=6$; $p<0.05$). Thus, during the lake surveys, effective fishing effort had been reduced in the larger lakes.

To examine the effect of varying fishing intensity on fish yield and catch per unit effort, we used individual values for each year for each lake rather than the means of the catch statistics and intensities. Thus, individual values of the variates from each lake were considered, for practical purposes, as independent from one another.

Overall, brook trout yield increased with increasing fishing intensity (Fig. 2A). Yield (Y) was a significant linear function of intensity (X) ($Y=0.117+0.192\ X$; $r=0.667$; $N=26$; $p<0.01$). A semilogarithmic transformation (Sokal and Rohlf 1969) improved the fit slightly ($Y=0.338+0.345$ log X; $r=0.714$; $N=26$; $p<0.01$), suggesting that increases in yields declined as intensity increased.

Deviations from the regression of yield on fishing intensity emphasized the similarities and differences in the relative abundance of brook trout among the study lakes (Fig. 2A). For example, the mean annual yield of brook trout from Sandy Pond was more than six times that from Candlestick Pond although mean annual fishing intensity in the two lakes differed only slightly (Table 1). In contrast, the difference in mean annual yield between Sandy Pond and Half Moon Pond was largely a result of the difference in mean annual fishing intensity (Fig. 2A).

Overall, catch per unit effort of brook trout decreased with increasing fishing intensity (Fig. 2B). The relationship between catch per unit effort (Y) and fishing intensity (X) could be described simply by a significant linear equation ($Y = 0.541 - 0.181\ X$; $r=0.412$; $N=26$; $p<0.05$), but outliers from Candlestick Pond obviously detracted from a simple description of the relationship. Exclusion of the data from Candlestick Pond resulted in a highly significant linear relationship ($Y=0.755-0.337\ X$; $r=0.813$; $N=22$; $p<0.01$), indicating that factors other than fishing intensity accounted for the comparatively low catch rates from Candlestick Pond.

Discussion

The deployment of effort in relation to lake size in our study was directly comparable with methods used in standard surveys of small lakes (i.e. Harvey 1975; Kelso and Gunn 1984; Kelso

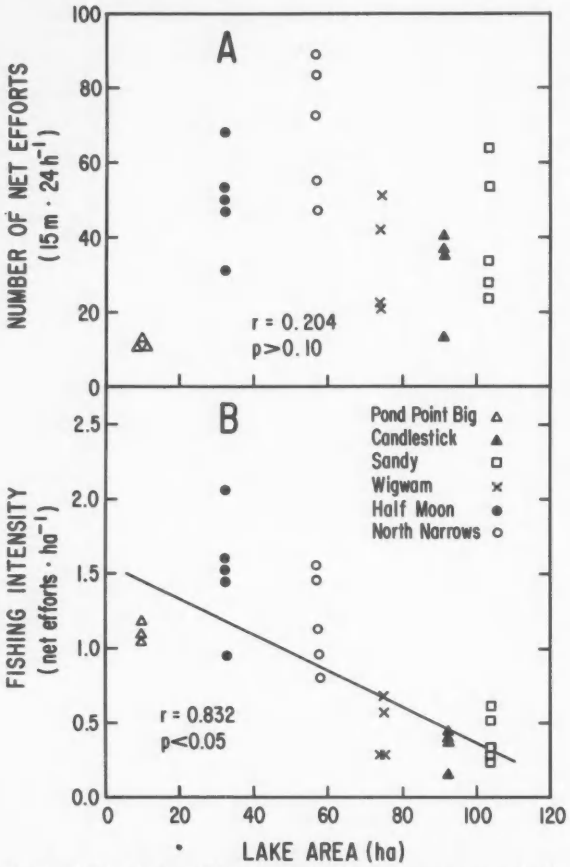

FIG. 1. Fishing effort and intensity during lake surveys compared with lake area in six lakes of Gros Morne National Park. Yearly values of effort and intensity in each lake are included. For comparisons among lakes, mean values of effort and intensity ($N = 6$) were regressed on area. Correlation coefficients and levels of significance for linear regressions are shown. Regression equations are presented in the text.

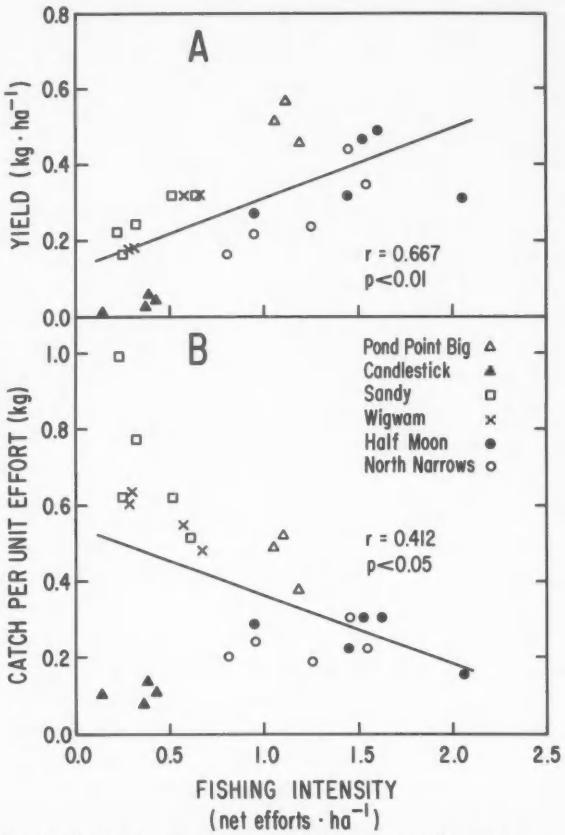

FIG. 2. Yield and catch per unit effort of brook trout during lake surveys compared with fishing intensity in six lakes of Gros Morne National Park. Correlation coefficients and levels of significance for linear regressions with individual values ($N = 26$) are shown. Regression equations are presented in the text.

et al. 1986). Obviously, if all available gear is deployed for a standard time, fishing effort will be constant as lake size varies but effective fishing effort or fishing intensity will decrease with increasing lake size. This pattern of gear deployment can be expected to result, as in the present study, in biased catch statistics with decreasing yield but increasing catch per unit effort associated with increasing lake size. The reasons for this bias have been well documented (Ricker 1975; Hamley 1980). A greater catch is expected from a given lake area if the amount of fishing effort is increased. The rate of increase in catch with increasing effort can be expected to decline as a local depletion of fish occurs. Conversely, as fishing effort in a given lake area is increased, a reduced catch per unit effort is expected simply as a result of an increased competition by the nets for a finite number of fish. These principles apply within an individual lake and, given the same relative abundance of fish, among lakes. Obviously, correction for such bias would improve the possibility of recognizing differences in the relative abundance of fish within and among lakes.

Correction for this bias can be made in a lake by applying a constant effort or intensity during repeated surveys. If other factors which influence catch (e.g. mesh size, net location, and season) can be kept constant, changes in fish abundance in that lake should be reflected in changes in both yield and catch per unit effort (Ryan 1984; Hamley and Howley 1985).

The application of a constant level of fishing intensity in all lakes may not always be practical. If this is the case, then deviations of yield and catch per unit effort from calculated regression lines could be used as measures of relative fish abundance among lakes. For example, yield and catch per unit effort of brook trout from Candlestick Pond were lower than expected on the basis of fishing intensity (Fig. 2) suggesting that trout abundance was comparatively low. This is consistent with the low pH in Candlestick Pond. Water with a pH of less than 5.5 is considered borderline for brook trout survival (Power 1980) and may result in reduced rates of growth (Rogers 1984). Low pH has been identified as a causative factor in the low production of other salmonids in Candlestick Pond (Rombough et al. 1978; Barbour et al. 1979).

The potential bias in catch data due to variable fishing intensity has long been recognized (Carlander 1955; Ricker 1975) but it has not become standard practice to correct for this bias during limnological surveys. In many surveys, this bias has been compensated for, to some extent, by the inclusion of lake area as an independent variable in multiple regression equations to

explain catch rates (Kelso and Gunn 1984; Kelso et al. 1986). However, this procedure does not account for differences in fishing effort among lakes. Correction of catch data for variable fishing intensity will improve the recognition of differences in fish abundance, particularly among small lakes. This correction can be made by the application of a constant fishing intensity during lake surveys or by the inclusion of fishing intensity as an independent variable in the analyses of survey data.

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Changes in Prey Rank and Preference by Young Planktivores for Short-Term and Long-Term Ingestion Periods

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Feeding by young planktivorous fishes (yellow perch, *Perca flavescens*, rainbow trout, *Oncorhynchus mykiss*, and lake trout, *Salvelinus namaycush*) was examined. Prey rank was determined by offering a swarm of one prey type and observing ingestion rates. During the initial feeding burst, larger prey generally ranked higher. During long-term feeding the largest prey, large *Daphnia magna*, generally declined in rank while the smallest prey, *Diaptomus sicilis*, increased to the highest or second highest rank. Prey preference was measured with fishes feeding in a swarm of mixed prey. Initially small rainbow trout and yellow perch selected for large *Daphnia* then switched to *Diaptomus*. For small rainbow trout this switch in prey preference paralleled the change in prey rank. For yellow perch, large *Daphnia* and *Diaptomus* provided essentially the same long-term ingestion rates. The nearly exclusive selection for *Diaptomus* during long-term feeding did not agree with prey rank based on caloric ingestion rates. Previous work has shown that yellow perch have a high growth efficiency on a diet of *Diaptomus*. Selection for *Diaptomus* suggests that fish can rank prey by nutritional quality as well as caloric ingestion rates.

L'alimentation de jeunes poissons planctivores (*Perca flavescens*, *Oncoryhnchus mykiss*, et *Salvelinus namaycush*) a été étudiée. L'ordre de consommation des proies a été déterminée en offrant un essaim d'organismes appartenant à un type de proie et en observant le taux d'ingestion. Pendant la poussée initiale d'alimentation, les grosses proies occupaient en général les premières places, comme *Daphnia magna*, occupaient en général un rang inférieur tandis que les petites proies comme *Diaptomus sicilis* atteignaient la première ou la seconde place. La préférence des proies a été mesurée chez des poissons se nourrissant dans un essaim de proies mélangées. Au début, les truites arc-en-ciel et les perchaudes de petite taille se nourrissaient de *Daphnia* de grande taille, puis de *Diaptomus*. Dans le cas de la truite arc-en-ciel de petite taille, ce changement de préférence était parallèle au changement de rang des proies. Dans le cas de la perchaude, les *Daphnia* et les *Diaptomus* de grande taille fournissaient essentiellement le même taux d'ingestion à long terme. Le choix presque exclusif de *Diaptomus* pendant la période d'alimentation à long terme ne concordait pas avec le rang des proies établi en fonction du taux d'ingestion de calories. Des travaux antérieurs ont montré que la croissance de la perchaure était plus grande lorsqu'elle se nourissait de *Diaptomus*. Le choix de *Diaptomus* porte à croire que les poissons peuvent choisir leur proie en fonction de la qualité nutritionnelle aussi bien qu'en fonction du taux d'ingestion de calories.

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Numerous studies of feeding by planktivorous fishes have used one of two approaches to predict prey selection. Several authors have evaluated optimal foraging models for fish that predict greater selectivity for prey that provide greater ingestion rates (e.g. Werner and Hall 1974; Werner 1974; Mittelbach 1981; Werner et al. 1983; Mills et al. 1984; Butler and Bence 1984; Li et al. 1985; and Bence and Murdoch 1986). Encounter frequency models predict greater selectivity for those prey that are more visible (Confer and Blades 1975; Eggers 1977; Wright and O'Brien 1984). Despite major differences between these two kinds of models, both predict that fish should select for the largest prey thay can rapidly swallow.

There is, however, increasing evidence that some planktivorous fish do not do this. *Gambusia* showed maximum selection for mid-sized *Daphnia* (Butler and Bence 1984). Young-of-the-year European perch, *Perca fluviatilus*, select smaller, more elusive copepods over larger and more readily captured *Daphnia* (Furnass 1979). Young yellow perch, *Perca flavescens*, select for mid-sized *Daphnia* as shown by field samples (Hansen and Wahl 1981; Mills et al. 1984) and laboratory experiments (Mills et al. 1984). Although young perch prefer mid-sized prey, zooplankton of a wide range of sizes have the same initial handling time so that larger *Daphnia* provide greater initial rates of ingestion (grams per time) (Mills et al. 1984).

The predictions of optimal foraging models, that planktivorous fish will select for larger prey, are based on measurements of ingestion rates by fish feeding briefly in a swarm of prey (see previous citations). Preference by small planktivores for smaller prey indicates that selection is influenced by more than the initial reward rate. Other factors that influence prey selection may involve digestive processes. Older literature reviewed by Paloheimo and Dickie (1966) showed differences in growth efficiency with different prey. Schalles and Wissing (1976) found large differences in the calorigenic effect of food pellets composed of different food types. Wankowski and Thorpe (1979) found that the growth efficiency of young Atlantic

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salmon, *Salmo salar*, varied with the prey size. Consumption of mid-sized prey resulted in the highest efficiencies, perhaps because of greater capture costs for smaller prey and greater digestive costs for larger prey. Gophen (1980) observed large differences in growth rates and assimilation efficiency for *Sarotherodon galilaeum* fingerlings fed different diets. Confer and Lake (1987) observed large differences in growth rates for young yellow perch fed equal rations (grams per day) of different zooplankton. Thus, nutrition may be significant to the feeding ecology of zooplanktivores.

Previously, Mills et al. (1984) speculated that the preference for smaller prey by young yellow perch during continuous feeding was related to the speed of digestion. Herein we examine this speculation. Prey rank and prey preference by several young fishes were observed during an initial feeding burst and during long-term ingestion. We equated prey rank to the relative amount ingested (joules) for timed intervals during trials with one prey. We determined prey preference with fishes feeding in a dense mixture of several prey types. We expected that the initial reward rate for small planktivores would be greater with larger prey as observed in earlier work (e.g. Mills et al. 1984). However, we hypothesized that the long-term reward rate would be greater with smaller prey, perhaps because of differences in digestive speed. We also hypothesized that fishes, offered a dense mixture of prey, initially would select for prey that ranked highest during an initial feeding burst, but subsequently would switch to prey that ranked highest during long-term feeding. Finally, we hypothesized that by switching prey preference, the total ingestion (joules) from a mixed swarm would approximate the sum of the highest initial ingestion plus the highest long-term ingestion as measured with the pure prey trials.

In a narrow sense, these experiments were designed to explain the seemingly implausible results that young yellow perch, which obtain the greatest reward rate during a feeding burst by selecting for large *Daphnia*, prefer mid-sized *Daphnia* during continuous feeding (Mills et al. 1984). In a broader sense these experiments test: if handling time is a constraint (i.e. a constant) or a variable that changes with gut fullness; if relative reward for different prey (i.e. prey rank) changes as gut fullness changes; and if small planktivores change the criteria (i.e. the attribute of the prey) by which prey are ranked as gut fullness changes.

Methods

The number of prey ingested by young-of-the-year fishes feeding in aquaria on different species and sizes of zooplankton was observed directly. We used the following species and sizes of fishes: yellow perch, 12 individuals of 34–43 mm total length; lake trout, five individuals of 50–57 mm total length; and rainbow trout, eight individuals of 32–39 mm total length and the same individuals observed again after growth to 41–50 mm total length. The trout, raised on a synthetic diet, were obtained from Tunison Laboratory of Fish Nutrition. Yellow perch, hatched from eggs taken from Oneida Lake, NY, and raised on a natural mixture of zooplankton, were provided by E. Mills. Experimental fish were maintained in seemingly healthy condition as evidence by growth rates on the order of 0.5 mm total length·d^{-1}. Observations were made during May–August 1987.

Fish were acclimated to experimental conditions and prey types for at least 2 wk, by which time they fed rapidly in the experimental aquaria on all prey types. These aquaria, 28 × 26 × 12 cm, were made of plexiglas with white sides and a transparent front. Each aquarium was aerated and was partially immersed in a larger tank that had filters, aerators, and a coolant coil. Screened holes in the sides of the experimental tank allowed some exchange of water. Water temperatures ranged from 16 to 18°C.

Experimental conditions provided an excellent view of each strike by the fish at a prey. Fluorescent overhead lights eliminated shadows in the aquaria. An opaque cloth hung from the front of the light fixture to the top of the front of each aquarium so that we were not "blinded" by direct light. The brightly illuminated fish and zooplankton were viewed against a clean, white background.

Fish were starved for 14–16 h before testing. Ambient light was dimmed during the night, and experiments were initiated about 3 h after light was returned to normal room illumination. For each set of observations, two fish were added to an experimental aquarium and left undistrubed until they appeared calm. Then, a swarm of prey was poured into the aquarium. During feeding the conditioned fish faced into a current from the aerator. As prey flowed by the fish, we observed each strike and determined if the prey were actually captured. Each data set, i.e. all the prey eaten by one fish during the observation periods of an experiment, was obtained by one of us watching one fish. Results for some fish were disregarded when a seemingly subordinant fish quit feeding, or when insufficient prey were available to complete the trial. A crash in the lake population of copepods limited the number of trials with these prey. A narrow range of fish total length was selected for analyses because diet changes with fish size (Mills et al. 1984). Thus, results from several fish of extreme size were disregarded. Emphasis was placed on yellow perch because of greater background knowledge about their prey selection.

Prey were always maintained at high densities by continual replenishment during all trials. Densities were high enough that several of the largest *D. magna* passed within a few centimetres of the fish between strikes even during the initial feeding burst. The abundance of smaller *Daphnia* and *Diaptomus* was several times greater than that for the large *Daphnia* during both single and mixed prey trials. Thus, while about four to five large *Daphnia* moved by the fish between each strike even during the feeding burst, perhaps 10–20 smaller prey of each type moved by the fish in the same time. These conditions allowed the fish to feed at a rate unlimited by prey abundance, and to freely select among prey in mixed prey trials. Densities were quantified for a few mock trials; i.e. trials without fish but with prey densities that appeared to match the experimental trials. Two such trials with large *D. magna* and two with small *D. magna* were set up, one of each by each author. The prey were removed and counted. These densities were 20 and 22·L^{-1} for large *D. magna* and 105 and 110·L^{-1} small *D. magna*.

Daphnia magna and *D. pulex* were grown in aquaria with an excess of algae. Nearly all *Daphnia* had oil droplets and adults usually carried eggs which indicated healthy animals with a high caloric value. *Diaptomus sicilis* were obtained from Fayetteville-Green Lake in Green Lakes State Park, Fayetteville, NY, and used within 4 d of collection. For each feeding trial, zooplankton were sorted to uniform size by gentle and repeated sieving through U.S.A. Standard Soil Testing sieves. More than 30 individuals of each zooplankton type for each trial were sized using a computerized recording procedure (Mills and Confer 1986). The lake samples of *Diaptomus* also contained a few *Epischura*. Sieving removed *Epischura* that were larger than

the *Diaptomus*, and reduced the *Epischura* abundance so that they usually were not detected in the sample measured for size.

Daphnia magna dry weight were estimated from a length–weight regression from Burns (1969). Dry weights for *D. pulex* and *Diaptomus* were estimated from the following weight (micrograms) to length (millimetres) regressions which we determined:

$$D.\ pulex \quad \text{Weight} = 9.5 \cdot L^{2.46}$$
$$D.\ sicilis \quad \text{Weight} = 5.3 \cdot L^{1.90}$$

Despite repeated sieving, the mean weight of nominally identical prey types decreased during the summer. Trials for each fish group were run consecutively, and completed within 2–3 wk. Within this time the variation of prey size for each fish group was small. The size range of each fish group, the number of replicate data sets, and the mean dry weight of each prey type follows: lake trout (50–57 mm total length), 3–4 replicates each for small, medium, and large *Daphnia magna* of 18, 55, and 266 μg, respectively; large rainbow trout (41–50 mm total length), 4–5 replicates each for small, medium, and large *D. magna* of 16, 42, and 258 μg, respectively; small rainbow trout (32–39 mm total length), 5–7 replicates each for small, medium, and large *D. magna* and *Diaptomus sicilis* of 12, 58, 233, and 6.1 μg, respectively; yellow perch (34–43 mm total length), 7–14 replicates each for small, medium, and large *D. magna*, small *Daphnia pulex*, and *D. sicilis* of 12, 76, 222, 16, and 4.2 μg, respectively. For small rainbow trout and yellow perch trials with pure and mixed prey types were temporally interspersed and prey weights for pure and mixed trials were virtually identical.

Caloric values for zooplankton were estimated from literature values summarized in Confer and Lake (1987). The estimated values, in joules per gram dry weight, were: 1199 for large *D. magna* and medium *D. pulex*, which usually were ovigerous; 1055 for all the smaller, preadult *Daphnia*; and 1328 for *Diaptomus*.

Feeding was observed constantly for the time intervals of 0–1, 1–5, and 5–10 min. By the end of this time, the initial feeding burst subsided greatly. Feeding was observed next from 55–60 min of the experiment, and that rate was used to estimate ingestion for 10–60 min. Long-term ingestion, i.e. ingestion after the first hour, was estimated with 5-min observations at hourly intervals from the end of the second to the fifth (small rainbow trout only) or sixth hour. These hourly values were summed to obtain the total long-term ingestion from 60 to 300 or 360 min.

The number of prey eaten was converted to joules. The mean amount ingested by replicate individuals for each fish type for each prey type for each time interval was determined. Prey rank was determined by comparisons of the mean amount ingested from trials when fish were offered only one prey type. For each fish type and time interval, the amount ingested by individual fish was used to determine statistical differences in prey rank. Using the individual values, a Kruskal–Wallis value was computed for paired comparisons of all combinations of prey types.

Gut passage times were determined for yellow perch utilizing the last meal of the day preceding an experiment (14–16 h before the trial) which consisted of prey that contrasted with the experimental prey; e.g. red *Diaptomus* 16 h before a trial with gray/pink *Daphnia*. During the trial, the initial fecal pellets had the color of the prey provided just before fasting. Gut passage time was equated to the length of time before the first release of a fecal pellet containing the experimental prey.

Results

Fish behavior changed greatly during the 5 or 6-h trials. Initially, the prey were pursued with vigor and rapidly ingested. Feeding rates declined rapidly. Generally the ingestion from 1–5 min was less than 4× the amount from 0–1 min, while the amount ingested from 5–10 min was almost always much less than from 1–5 min (Table 1). By 1 h the fish had bulging guts and usually remained motionless between lethargic strikes while the current brought prey to them. Prey were swallowed slowly, sometimes after considerable mouthing.

The initial burst of feeding declined so rapidly that the total ingestion for each prey type during long-term feeding (60–360 min) usually greatly exceeded ingestion during the first 10 min of feeding. The one exception was small rainbow trout feeding on large *D. magna*. While many previous studies of prey selection have emphasized the initial feeding burst, in our experimental design the long-term feeding contributed more to the total diet.

Prey Rank with Pure Prey Types

Prey rank was measured for the initial feeding burst and for sustained feeding. Inspection of Table 1 shows that prey rank for the time intervals of 0–1, 1–5, and 5–10 min were virtually identical. To base statistical tests on the largest sample size, the initial prey rank was determined with the total ingestion for 0–10 min.

For the three trout groups, the amount ingested during 0–10 min increased with increasing *Daphnia* size (Fig. 1, 2 and 3). However, for all three fishes only the ingestion of large and small *Daphnia* was significantly different ($p<0.05$). Prey rank did change from the initial to the long-term feeding. During long-term feeding the ingestion of medium-sized *Daphnia magna* exactly equaled or was higher than ingestion for large *D. magna*. Within each of these three fish groups, ingestion during sustained feeding on the three *Daphnia* sizes was similar and statistically indistinguishable.

Small rainbow trout were also tested with *Diaptomus* as well as the three sizes of *D. magna*. *Diaptomus* was the smallest prey, and the initial ingestion rate of *Diaptomus* was lower than that for any *Daphnia* size ($p<0.01$). This continued the trend of decreasing initial ingestion rate with decreasing prey size (Fig. 3). Prey rankings during long-term feeding were the exact inverse of the initial rankings. Long-term reward rates for *Diaptomus* were significantly greater than for small and large *D. magna* ($p<0.01$) and for medium *D. magna* ($p<0.05$).

Prey rankings for yellow perch were similar to rankings for small rainbow trout. The reward during the first 10 min with the smallest prey, *Diaptomus*, was lower than with medium or large *D. magna* ($p<0.05$). During the initial feeding burst yellow perch could not swallow large *D. magna* as rapidly as medium sized *D. magna* or *D. pulex*. The larger prey were close to the gape limit of the perch, which could limit the ingestion rate (Werner 1974; Bence and Murdoch 1986).

For yellow perch, as with the trout, prey rank changed from the initial feeding to long-term feeding. *Diaptomus* was particularly noteworthy (Fig. 4). Initially *Diaptomus* ranked fifth of six prey types. During long-term feeding *Diaptomus* provided the second highest reward which was 98% of the maximum as obtained with large *D. magna* (Table 1). However, during long-term feeding the reward rates among prey types were similar,

TABLE 1. Average ingestion (joules) by small planktivores feeding in a swarm of prey. Ingestion after 10 min estimated from 5-min. observations at hourly intervals. n = number of fish. Mean weights of zooplankton for Mix A and Mix B given in Fig. 3 and 4.

Prey		Joules ingested during time interval (min)						
Species	mg/mm	0–1	1–5	5–10	10–60	60–360	0–360	n
Lake trout (50–57 mm)								
Small *Daphnia magna*	18/1.2	0.4	1.0	0.8	3.0	9.4	14.6	4
Medium *Daphnia magna*	55/1.8	1.4	1.5	0.8	5.1	10.6	19.4	4
Large *Daphnia magna*	266/3.2	3.6	1.5	0.6	2.4	10.6	18.6	4
Rainbow trout (41–50 mm)								
Small *Daphnia magna*	16/1.1	0.3	0.6	0.4	2.5	3.0	6.7	3
Medium *Daphnia magna*	42/1.6	1.7	1.7	0.9	2.0	17.8	24.0	2
Large *Daphnia magna*	258/3.2	3.8	3.0	1.0	5.0	12.4	25.2	5
Rainbow trout (32–39 mm)								
Diaptomus sicilis	6.1/1.1	0.1	0.4	0.5	2.8	10.5	14.2	6
Small *Daphnia magna*	12/1.0	0.3	0.6	0.4	0.7	2.4	4.4	6
Medium *Daphnia magna*	58/1.8	1.1	0.9	0.3	0.7	2.3	4.6	6
Large *Daphnia magna*	233/3.1	2.3	1.3	0.9	0	1.9	6.4	7
Mix A		1.7	1.8	0.9	6.4	14.7	25.5	4
Yellow Perch (34–43 mm)								
Daphnia sicilis	4.2/0.9	0.2	0.8	0.7	2.9	8.6	13.2	14
Small *Daphnia magna*	12/1.0	0.3	0.5	0.2	0.3	1.5	2.8	3
Small *Daphnia pulex*	15.5/1.2	0.5	1.6	1.1	1.9	5.0	10.4	6
Medium *Daphnia pulex*	58/2.1	2.0	1.4	1.3	1.6	7.3	14.2	5
Medium *Daphnia magna*	76/2.0	2.0	1.6	0.8	1.8	6.6	12.8	8
Large *Daphnia magna*	222/3.0	1.2	1.0	0.6	1.4	8.8	13.0	7
Mix A		1.3	0.8	0.8	5.0	14.5	22.4	7
Mix B		2.2	1.5	0.9	4.3	12.5	21.5	6

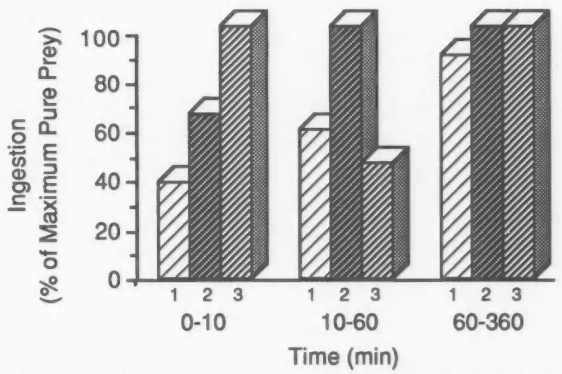

FIG. 1. Ingestion rates by lake trout feeding for three consecutive time periods on one of three prey types. Values were obtained with small, medium, and large *Daphnia magna*, bars 1–3, respectively. Results are expressed as a percentage of the maximum reward (joules) with a pure prey type during each time interval. Details in text.

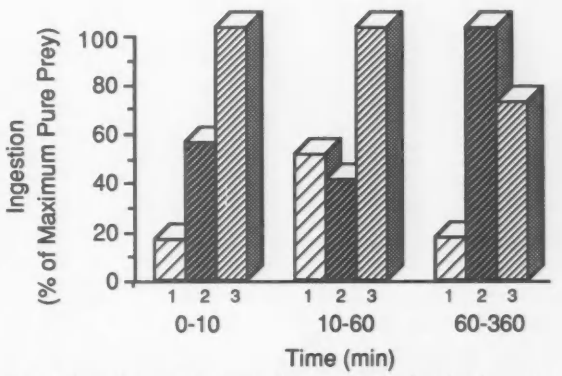

FIG. 2. Ingestion rates by large rainbow trout feeding for three consecutive time periods on one of three prey types. Values were obtained with small, medium and large *Daphnia magna*, bars 1–3, respectively. Results expressed as in Fig. 1. Details in text.

and only small *D. magna* provided a statistically lower ingestion than any other pure prey type.

Gut passage times were estimated with young yellow perch. *Diaptomus* had a mean passage time of 180 min (range = 160–200 min, $n = 5$). The *Daphnia* passage times with a mean of approximately 300 min (range = 235–360 min, $n = 13$) were much greater than for *Diaptomus*. The longest passage time for *Diaptomus* was shorter than the shortest time for *Daphnia*. The change in prey rank and this difference in gut passage time support our second hypothesis that the prey which was digested most rapidly would also provide the greatest reward during long-term ingestion.

Prey Selection from Mixed Prey

Prey preference was tested with fishes offered a high density of three prey types at a time. We tested whether prey preference changed from the initial burst to the long-term feeding, and whether the changes in preference paralleled the changes in

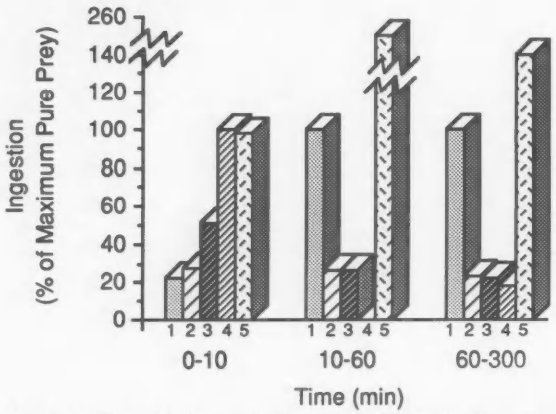

FIG. 3. Ingestion rates by small rainbow trout feeding for three consecutive time periods on one of four prey types or a mixture of three prey types. Values were obtained with *Diaptomus sicilis*, small, medium, and large *Daphnia magna*, and Mix A, bars 1–5, respectively. Results expressed as in Fig. 1. Details in text.

prey rank. Small rainbow trout and yellow perch were offered a mixture of small and large *D. magna* and *Diaptomus* (Mix A). Yellow perch were offered an additional mixture of large *D. magna*, small *D. pulex*, and *Diaptomus* (Mix B).

Trends in the results were the same for both fishes and both mixes (Table 2). Initially, there was a strong preference for *Daphnia*. During the first minute of feeding three of four rainbow trout and 10 of 13 yellow perch ate more *Daphnia* than *Diaptomus*. Twelve of the 13 fishes that preferred *Daphnia*, ate more large than small *Daphnia*. One trout and six perch ate only *Daphnia* during the first minute of feeding, but no fish ate only *Diaptomus*. As hypothesized, the fishes feeding in a mixture of prey selected initially for the prey that provided the highest initial reward as a pure prey type.

During the first 10 min of feeding, most fish showed a transition in the size of *Daphnia* that was preferred. Comparing the first minute to the first to fifth minutes, the ratio of small to large *Daphnia* eaten increased for all four trout and 9 of 13 perch. The proportion of small to large *Daphnia* continued to increase during the fifth to tenth minute. Of three trout and eight perch that ate no large *Daphnia* during this time, seven fish did eat small *Daphnia*.

During long-term feeding, every fish ate *Diaptomus* almost exclusively. Almost all of the fish switched within 10 min of the start of the feeding. Individual fish switched to *Diaptomus* at different times, and the abruptness of the transition shown by most individual fish is not reflected in the average values of Table 2.

Reward Rates from Mixed Prey

Total ingestion with mixtures of prey were considerably higher than ingestion with any pure prey type (Fig. 3 and 4). We predicted that the total ingestion from a mixture of prey would approach a hypothetical maximum obtained by summing the highest ingestion for any prey type for consecutive observation periods. For small rainbow trout feeding on pure prey, the highest values for any prey for the consecutive time periods were: 48.5 J for 0–10 min with large *Dapnia*, 184 J for 10–60 min with *Diaptomus*, and 43.9 cal for 60–300 min with *Diaptomus*. The sum of these values, 233 J, provided the hypothetical maximum ingestion for feeding on the mixture of prey. However, ingestion with mixed prey showed something analogous to a synergistic effect. For the above example, the actual ingestion from the mix was 446 J. For both fishes and both prey mixtures, the actual ingestion exceeded the hypothetical maximum by 30–90%. Almost all of this excess was due to greater ingestion of *Diaptomus* during the long-term feeding in the mix than in the pure prey trial. During long-term feeding the ingestion of *Diaptomus* from the mixed prey trials was nearly 50% greater than ingestion of *Diaptomus* from pure prey trials. The density of *Diaptomus* of both pure and mixed prey trials was maintained high enough that fish passed up several prey brought to them by currents between every feeding strike. Thus, ingestion during both the pure and the mixed trials was never limited by the fish using time to search for a preferred prey type. Trials with pure prey and mixed prey were temporally interspersed and used the same individual fish. Thus, the higher ingestion of *Diaptomus* during the mixed prey trials does not seem to be an artifact of a sampling regime. The much greater ingestion from the mix was consistent among individual fish and between fishes.

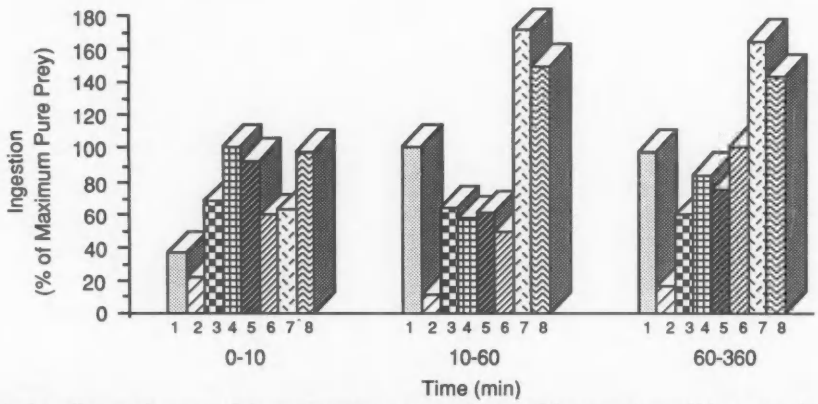

FIG. 4. Ingestion rates by yellow perch on one of six pure prey types or two mixtures of three prey types. Values were obtained with *Diaptomus sicilis*, small *Daphnia magna*, small *Daphnia pulex*, medium *Daphnia pulex*, medium *Daphnia magna*, large *Daphnia magna*, Mix A, and Mix B, bars 1–8, respectively. Results expressed as in Fig. 1. Details in text.

TABLE 2. Species of prey ingested during timed intervals by small planktivores feeding in a swarm of mixed prey types. All prey types were maintained at high density by replenishment. Values are the mean and standard deviation for the number of prey ingested by seven (Mix A) or six (Mix B) yellow perch and four rainbow trout. Weights given in Figs. 3 and 4.

		Number of Prey Ingested from Mixtures					
		Mix A					
		Large		Small			
Species	Time (min)	*Daphnia magna* Mean	SD	*Daphnia magna* Mean	SD	Diaptomus sicilis Mean	SD
Yellow perch	0–1	3.4	1.51	3.0	2.08	4.71	6.97
	1–5	1.0	1.41	2.86	4.38	60.57	59.56
	5–10	0.43	1.12	5.57	7.68	88.57	65.29
	10–60	0	0	3.0	1.91	70.14	29.83
	60–360	0	0	3.0	4.04	162.71	45.19
Rainbow trout	0–1	5.0	1.91	2.50	1.00	3.75	5.56
	1–5	3.50	5.07	7.75	1.71	18.0	33.35
	5–10	0.75	1.50	4.75	4.27	28.0	44.27
	10–60	0	0	1.0	0.82	48.50	51.76
	60–300	0.25	0.50	2.75	2.06	74.50	69.12
		Mix B					
		Large		Small			
		Daphnia magna Mean	SD	*Daphnia pulex* Mean	SD	Diaptomus sicilis Mean	SD
Yellow perch		6.83	2.14	0.33	0.52	2.33	3.93
		4.33	2.34	3.17	2.48	16.0	25.90
		1.67	1.51	5.67	4.03	47.67	57.14
		0	0	4.83	3.37	72.83	37.47
		0	0	8.17	7.88	181.17	111.58

Discussion

Foraging by young planktivores during the first 30 s or 1–2 min of a feeding burst have been used to rank prey and/or test predictions of prey preference (e.g. Werner 1974; Mittelbach 1981; Werner et al. 1983; Mills et al. 1984; Butler and Bence 1984; Li et al. 1985; Bence and Murdoch 1986). It has been assumed that it is more "appropriate to measure ... profitability using starved fish ..." (Bence and Murdoch 1986). However, it has not been tested whether the initial prey rank applied to continuously feeding fish.

Under the conditions of our laboratory experiments, prey rank by continuously feeding fish changed greatly from the initial to the long-term feeding. Differences in prey rank for these two time periods can be better understood by considering the components of the time budget during feeding. The time budget includes the time necessary for search, capture and ingestion, and digestive pause (Holling 1966). Feeding in a dense swarm of prey eliminates search time. Feeding for only 30 s to 2 min after a half-day of starvation, eliminates digestive pause. Capture time, i.e. the time used to the strike at prey, was very brief. During the feeding burst the time budget and determination of the prey rank were dominated by the time required to swallow prey. Thus, the prey quality that determined the initial prey rank was the speed of swallowing various prey items.

We used the same currency, joules ingested per time, to measure prey rank for the initial and long-term feeding. However, the much slower ingestion rates during long-term feeding were not determined by the maximum speed of swallowing. During long-term feeding ingestion approached a steady state and the digestive pause between swallowing prey became the most significant component of the time budget. Thus, the prey quality that determined the long-term prey rank was the speed of digestive processing.

These results suggest that two criteria, maximizing the speed of swallowing and minimizing the digestive pause, are applicable to prey selection. Initially, the largest prey provided the greatest rate of swallowing. During long-term feeding smaller prey seemed to provide some digestive advantage for all four species size groups of small fish. Most small, young planktivores swallow prey whole and have incompletely differentiated digestive tracts. Such fish may be able to digest small prey more rapidly, as shown by the difference in gut passage times by yellow perch for *Diaptomus* and *Daphnia*.

If prey preference is optimized for ingestion rates, then changes in prey rank as fish fill their guts should lead to changes in prey preference. Small rainbow trout switched preference from large *Daphnia* to the smallest prey, *Diaptomus*. This exactly matched the change in prey rank from the initial to the long-term feeding (Fig. 3).

The yellow perch, as with the trout, initially ate only large *Daphnia* and ultimately ate *Diaptomus* nearly exclusively. Unlike with the trout, the nearly exclusive consumption of *Diaptomus* during long-term feeding is contrary to the prey rank. According to the prey rank the fish should have shown a preference for large *Daphnia* or perhaps about equivalent preference for *Daphnia* and *Diaptomus* since the amounts ingested were so similar (Fig. 4). Thus, prey preference must have been influenced by some factor in addition to prey rank as measured in joules ingested.

Confer and Lake (1988) measured the growth rate of young yellow perch offered the same mass of different species of zoo-

plankton. For each of four experiments, the growth of yellow perch feeding on *Diaptomus* was always considerably higher than growth on the same mass of large *Daphnia magna*. In this current study, yellow perch selected for the prey that previously had resulted in the highest growth efficiency. Ingestion rate weighted by a factor for growth efficiency would correctly predict the strong preference for *Diaptomus*.

The degree of gut fullness at which these laboratory fish switched prey preference suggests conditions under which fish in situ might do likewise. The small rainbow trout switched to eating *Diaptomus* nearly exclusively near the end of 5 min of feeding. During the first 5 min these fish ingested an average of 18 *Daphnia magna*. After 300 min of feeding these fish ate an additional mass of *Diaptomus* that was 3 to 10× larger than the mass of *Daphnia* ingested by individual fish after 5 min. Gut passage times were not quantified for young rainbow trout, but fecal pellets first appeared only near the end of 300 min. Thus, the small rainbow trout switched prey preference when their guts were about 1/4 to 1/11 full. Perhaps small rainbow trout in situ will do the same.

In this study young yellow perch switched to *Diaptomus* after eating as few as two to as many as 19 large *Daphnia magna*. Field samples of yellow perch from Oneida Lake showed that fish averaged 13 *Daphnia pulex* in their guts (Figure 6 of Mills et al. 1984). The range in the amount of prey in the guts of these field fish overlapped with the gut fullness at which laboratory fish changed prey preference. Perhaps young yellow perch in situ will change the criteria by which prey are ranked within the range of prey densities that occurs naturally.

Switching the criteria for determining prey rank leads to a mixed diet even if the fish are feeding in a swarm of prey. Pulliam (1975) predicted a mixed diet for a predator when feeding under nutrient constraints. However, this similarity is only superficial. We predict that initially a fasted fish should take only the prey that maximizes swallowing. When the fish is moderately full, and after a period of transition, we predict that a fish should take only the prey that is digested most rapidly. The factors considered by Pulliam lead to a prediction that a predator should occasionally select a prey that provides some unusual but essential nutrient. However, this model does not require that a predator in a fine grained environment initially take only one prey type and then switch to another prey type. In our study young yellow perch initially ate only large *Daphnia*, and, after a transition period, ate *Diaptomus* almost exclusively. The rainbow trout showed a similar pattern. Thus, the results approximate an all-or-none selection with alternating criteria and prey rank.

Earlier models of prey selection by young planktivores assumed that prey rank could be estimated from the initial feeding burst. This current study showed that prey rank and preference changed rapidly and greatly. Similar changes may occur in situ as follows. Young planktivores in lakes of low prey density or at dawn in eutrophic lakes will have few prey in their guts and may select for large prey. Gut contents will increase after sunrise, and in eutrophic lakes may reach a level that the fishes switch to smaller prey. By so doing they would initially select prey that maximize the speed of swallowing, and then alternate criteria and select prey that minimize digestive pause and/or provide the greatest growth efficiency.

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Maximum Likelihood Estimation of Water Quality Concentrations from Censored Data

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Concentration data for water quality parameters reported as less than the detection limit (DL) may be considered to have come from a censored probability distribution. Traditionally, if it was necessary to assign a value to a sample reported as less than DL, various ad hoc methods were used such as selecting arbitrary values (0, 1/2 DL, DL, etc.). As analytical methods improved, DL's became smaller and the choice of ad hoc methods had less of an effect. However, there are two cases where the choice of estimation method is still a problem: (1) it is desired to calculate a differential loading (i.e. downstream minus upstream); (2) a loading estimate is desired in a tributary whose flow rate is extremely large. Both cases apply in connecting channels such as the Niagara and Detroit Rivers. The background for development of a nonarbitrary method for handling these situations is presented and the resultant estimator is used on water quality data from the connecting channels and Lake Ontario. The equations for confidence intervals for estimated mean concentrations or loadings are also presented. The effect of changing the DL is discussed.

On peut considérer que les données de concentration relatives aux paramètres sur la qualité de l'eau indiquées comme inférieures au seuil de détection proviennent d'une distribution de probabilité tronquée. Traditionnellement, si l'on devait attribuer une valeur à un échantillon dont la concentration était inférieure au seuil de détection, différentes méthodes spéciales étaient utilisées comme le choix de valeurs arbitraires (0, 1/2 du seuil de détection, seuil de détection, etc.). À mesure que les méthodes d'analyse se perfectionnaient, les seuils de détection devenaient plus faibles et le choix de méthodes spéciales avait moins d'importance. Toutefois, il existe encore deux cas où le choix de la méthode d'estimation pose un problème : (1) lorsque l'on souhaite calculer une charge différentielle (c'est-à-dire la concentration en aval moins la concentration en amont); (2) lorsqu'il faut une estimation de la charge dans un tributaire dont le débit est très grand. Les deux cas s'appliquent dans le cas de cours d'eau qui servent à relier des plans d'eau comme les cours d'eau Niagara et Détroit. Le présent article présente les données de base nécessaire pour élaborer une méthode non arbitraire pour régler ces situations et l'estimateur résultant est utilisé pour les données sur la qualité de l'eau des cours d'eau qui servent à relier des plans d'eau et le lac Ontario. Les équations pour les intervalles de confiance pour estimer les concentrations moyennes ou les charges sont également présentées. On étudie du changement de seuil de détection.

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As the priority for chemical analysis of surface waters changed in the late seventies from nutrients and conventional parameters to metals and halogenated organics, the importance of a consistent method to handle values reported as "less than detection limit" has increased. This is true for two reasons. One is that biological effects in response to loadings of these contaminants occur at extremely low exposure levels such as parts per trillion and lower. The classical example of this is bioaccumulation of chlorinated organics in fish from water bodies that were previously considered clean (Edwards 1987; Opperhuizen et al. 1988; Swackhamer and Hites 1988). The other reason is that many of these new parameters are lognormally distributed in nature and a high proportion of "low" values are expected.

Statistical methods are therefore required to provide point estimates and confidence intervals for data aggregated in space or time when some values are reported as less than. Such estimates or summary values are compared with objectives and criteria, limits, previously established trend lines, and known biological requirements. The method of maximum likelihood provides a unified way to handle data from normal or lognormal distributions with or without some values reported as less than detection limit. In statistical terminology, values reported as less than are considered censored, with the detection limit being the point of censoring. Censoring can be of two types, Type I and Type II. In Type I censoring, the number of censored values is, itself, a random variable, while in Type II censoring a set percentage of values are censored Cohen (1959). Censoring can be at the right or left of the distribution. For water quality applications, the usual case in Type I censoring on the left, but the methods presented in this paper can be easily extended to the other cases.

During recent years, the estimation of the levels of many metals and organic contaminants in receiving waters from Type I censored data has received considerable attention. Gilliom and Helsel (1986) and Helsel (1986) suggested the use of the log-probability regression (LR) method to estimate the mean and variance from censored water quality data while El-Shaarawi (1988) recommended the use of the method of maximum likelihood (ML) instead. The LR method is simple and can be used as a short cut method but its use results in losing information by ignoring the detection limit and producing inadmissible estimates for the censored data. Also, formulas for the standard errors of the LR estimates are not available. On the other hand, the advantages of the ML estimates are well known, the most important being the properties of asymptotic efficiency and unbiasedness. Also, the method leads automatically to the estimation of the asymptotic variances and covariances of these estimates through the computation of the expected or the observed Fisher Information matrix. El-Shaarawi (1988) showed that the mean square error of the ML-estimators is significantly smaller than the variance of the best linear unbiased estimators when sample sizes are larger than $n = 10$. Since LR estimates belong to the class of linear estimates, the ML method provides a more efficient approach to estimating the mean and the variance of the population. But the actual computing of the ML estimates is considerable, including iterative solutions of the likelihood equations with convergence problems (Schneider 1986). Cohen (1961) gives a table which allows the computation of the ML estimates without performing the iterative process. However, as pointed out by David (1981) the table is subject to interpolation and may not be adequate for routine use.

Tiku (1967) derived estimators for the mean and standard deviation from Type II censored normal data by approximating the likelihood function. These estimators are easy to compute, seem to be as efficient as the maximum likelihood estimators, and are better than the best linear unbiased estimators.

In this paper the method of Tiku is applied to approximate the likelihood function for Type I censored normal data. Because water quality data are commonly represented by the lognormal distribution, special attention is given for deriving point estimates and confidence limits for the lognormal mean. Also, the method is applied to estimate the input of several contaminants to the Niagara and Detroit Rivers and the water column concentrations of two contaminants in Lake Ontario.

Our Appendix contains a numerical example using Detroit River total phosphorus data. The method has been programmed in three languages: FORTRAN IV, APL, and SAS. Copies of the source code are available from the authors upon request.

Statistical Methods

1. Likelihood Function

Suppose that out of N water samples, n_0 samples have concentrations less than X_0, the detection limit, and the remaining $n = N - n_0$ samples have the concentrations $X_1,\ldots,X_n$. Assuming the X_i's ($i = 1,\ldots,n$) are independent with a common lognormal distribution, hence $y_i = \ln X_i$ is normal. Let μ and σ^2 be the mean and the variance of y_i. The likelihood function for μ and σ is:

$$L = \frac{N!}{n_0!n!}\,[\Phi(\xi)]^{n_0}(2\pi\sigma^2)^{-n/2}\exp\left[-\sum_{i=1}^{n}\frac{(y_i-\mu)^2}{2\sigma^2}\right],$$

where $\xi = \dfrac{y_0-\mu}{\sigma}$ and $\Phi(\xi) = \dfrac{1}{\sqrt{2\pi}}\displaystyle\int_{-\infty}^{\xi} e^{-x^2/2}dx.$

The *ML* estimates $\hat{\mu}$ and $\hat{\sigma}$ are the values of μ and σ which satisfy the equations

$$(1)\quad \frac{\partial \ln L}{\partial \mu} = -\frac{n_0}{\sigma}\,g(\xi) + \frac{n(\bar{y}-\mu)}{\sigma^2} = 0 \text{ and}$$

$$(2)\quad \frac{\partial \ln L}{\partial \sigma} = -\frac{n_0\xi}{\sigma}\,g(\xi) - \frac{n}{\sigma} + \sum_{i=1}^{n}(y_i-\mu)^2/\sigma^3 = 0,$$

where $\bar{y} = \displaystyle\sum_{i=1}^{n} y_i/n$ and $g(\xi) = \dfrac{e^{-\xi^2/2}}{\sqrt{2\pi}\,\Phi(\xi)}$.

2. Modified Likelihood Equations

Tiku (1967) approximates $g(\xi)$ by $\beta_0 + \beta_1\xi$ when ξ is in the interval (a, b) where

$$\beta_1 = (g(b) - g(a))/(b - a) \text{ and } \beta_0 = g(a) - a\beta_1.$$

The values of a and b are determined as

$$a = \Phi^{-1}\left[p - \sqrt{p(1-p)/N}\right] \text{ and}$$

$$b = \Phi^{-1}\left[p + \sqrt{p(1-p)/N}\right],$$

where $p = n_0/N$ and Φ^{-1} is the inverse of Φ.

Replacing $g(\xi)$ in equations (1) and (2) by its approximation yields the modified likelihood equations

$$(3)\quad \frac{\partial \ln L}{\partial \mu} \simeq \frac{\partial \ln Lm}{\partial \mu} = -\frac{n_0}{\sigma}(\beta_0 + \beta_1\xi) + \frac{n(\bar{y}-\mu)}{\sigma^2} = 0$$

and

$$(4)\quad \frac{\partial \ln L}{\partial \sigma} \simeq \frac{\partial \ln Lm}{\partial \sigma} = -\frac{n_0\xi}{\sigma}(\beta_0 + \beta_1\xi) - \frac{n}{\sigma} + \sum_{i=1}^{n}\frac{(y_i-\mu)^2}{\sigma^3} = 0,$$

where Lm is the modified likelihood.
This leads to

$$\hat{\mu} = \frac{\bar{y} - h\beta_1 y_0 - h\beta_0\hat{\sigma}}{1 - h\beta_1}$$

and $\hat{\sigma}$ is the positive root of the quadratic equation

$$\hat{\sigma}^2 - s^2 - (\bar{y} - \hat{\mu})^2 + h\xi(\beta_0 + \beta_1\xi)\hat{\sigma}^2 = 0,$$

where $h = n_0/n$ and $s^2 = \dfrac{1}{n}\displaystyle\sum_{i=1}^{n}(y_i - \bar{y})^2$.

Finally, the variance–covariance matrix of $\hat{\mu}$ and $\hat{\sigma}$ is obtained

$$V = \frac{\hat{\sigma}^2}{n}\begin{pmatrix} (1 - h\beta_1) & \dfrac{2(\bar{y}-\hat{\mu})}{\hat{\sigma}} - h(\beta_0 + 2\beta_1\xi) \\ \dfrac{2(\bar{y}-\hat{\mu})}{\hat{\sigma}} - h(\beta_0 + 2\beta_1\xi) & 3\,\dfrac{(s^2 + (\bar{y}-\hat{\mu})^2)}{\hat{\sigma}^2} - 1 - h\xi(3\beta_1\xi + 2\beta_0) \end{pmatrix}^{-1}$$

$$= \begin{bmatrix} V_{11} & V_{12} \\ V_{21} & V_{22} \end{bmatrix},$$

where

$$V_{11} \simeq V(\hat{\mu}) \quad , \quad V_{22} \simeq V(\hat{\sigma}) \text{ and}$$

$$V_{21} = V_{12} = \text{Cov}\,(\hat{\mu}, \hat{\sigma})$$

The *ML* estimate (MLE) for normally distributed data is the pair of values of $\hat{\mu}$ and $\hat{\sigma}^2$ from the above equations. For lognormally distributed data, the *ML* equations are applied to the log-transformed data. The *ML* estimate of the lognormal mean $\alpha = e^{\mu + 1/2\sigma^2}$ is

(5) $\hat{\alpha} = e^{\hat{\mu} + 1/2\hat{\sigma}^2}$ and its variance is estimated by

(6) $\text{var}(\hat{\alpha}) = \hat{\alpha}^2 Q$ where

(7) $Q = V_{11} + 2V_{12}\hat{\sigma} + \hat{\sigma}^2 V_{22}$.

El-Shaarawi (1988) has shown that $\hat{\alpha}$ is asymptotically unbiased and a consistent estimate for α. A correction for bias may be made by:

(8) $\alpha = \hat{\alpha} \exp\{-Q/2\}$.

Approximate 95% confidence limits for α are

(9) $\hat{\alpha} \exp\{-1.96\sqrt{Q}\}$ and $\hat{\alpha} \exp\{1.96\sqrt{Q}\}$.

If no values are censored, then the estimators reduce to the ordinary MLE equations for normal or lognormal distributions.

(10) Normal: $\hat{\mu} = \bar{X}$ and $\hat{\sigma}^2 = \frac{1}{n}\sum_{i=1}^{n}(X_i - \bar{X})^2$

(11) Lognormal: $\hat{\mu} = \bar{y}$ and $\hat{\sigma}^2 = \frac{1}{n}\sum_{i=1}^{n}(y_i - \bar{y})^2$,

with equations (5)–(8) still applicable for "back-transforming" to observation space.

When comparing different areas of a lake or river or the same area at different times, it is often desirable to perform a *t*-test so that statements can be made about the significance of differences. The use of maximum likelihood methods provides a general framework not only for estimating parameters, but also for testing different hypotheses about the values of these parameters. In the present case we are interested in making inferences about the mean and the ratio of two means from lognormally distributed data.

3. Approximate Test for the Equality of two Lognormal Means

Suppose that we have two lognormal populations with means α_1 and α_2 and that we are interested in testing the null hypothesis H_0: $\alpha_1 = \alpha_2$ which is the same as testing H_0: $\rho = \alpha_1/\alpha_1 = 1$. Given a sample from each of the two populations, compute $\hat{\alpha}_1$ and $\hat{\alpha}_2$, the estimates of the means of the two lognormal populations, α_1 nad α_2. Also, from equation (7), compute Q_1 and Q_2. Then the approximate 95% confidence limits for ρ are:

(12) $\hat{\rho}_L = \frac{\hat{\alpha}_1}{\hat{\alpha}_2} \exp\{-1.96\sqrt{Q_1 + Q_2}\}$ and

$$\hat{\rho}_U = \frac{\hat{\alpha}_1}{\hat{\alpha}_2} \exp\{1.96\sqrt{Q_1 + Q_2}\}.$$

If the limits include the value $\rho = 1$, then H_0 is accepted.

Under the assumption of no association between flow and concentration, the confidence limits for the ratio of the upstream to downstream load can be obtained from equation (12) by multiplying the limits by the ratio of the flows.

In the case of no censoring, analysis is done as in Land (1972).

Applications

Table 1 presents the results of applying the maximum likelihood estimate method to contaminants data from the Niagara and Detroit Rivers and Lake Ontario. These examples were

TABLE 1. Summary of example applications.

							Confidence interval				
	N	n_0	X_0	$\hat{\mu}$	$\hat{\sigma}$	α	Lower	Upper	V_{11}	V_{22}	V_{12}
Niagara River											
Alpha-chlordane(ng·L^{-1})											
Niagara-on-the-Lake	33	20	0.05	−3.2964	1.088	0.0649	0.0414	0.108	0.0735	0.0590	−0.0384
Fort Erie	34	24	0.05	−3.6108	1.171	0.0517	0.0316	0.0911	0.1300	0.0959	−0.0802
Gamma-chlordane(ng·L^{-1})											
Niagara-on-the-Lake	33	30	0.05	−5.394	1.753	0.0178	0.0068	0.0660	2.139	0.814	−1.228
Fort Erie	34	27	0.05	−4.747	2.149	0.0574	0.0145	0.5260	0.790	0.486	−0.510
Lake Ontario											
1,1,1-Trichloroethane(ng·L^{-1})	81[a]	6	0.5	1.0720	0.728	3.792	3.183	4.55	0.0066	0.0038	−0.00019
Bromodichloromethane(ng·L^{-1})	82	52	0.5	−1.3529	2.339	3.206	1.093	14.55	0.1540	0.1270	−0.08810
Detroit River											
PCB congener 191(ng·L^{-1})[b]											
Grosse Ile	14	0	0.003	−4.7692	0.3643	0.00902	0.00744	0.01105	0.00948	0.00271	0
Windmill Point	13[c]	5	0.003	−6.0716	0.8293	0.00314	0.00191	0.00556	0.11340	0.08940	−0.06046
Phosphorus (mg·L^{-1})											
Grosse Ile	14	0	0.0023	−4.17	0.203	0.0157	0.0142	0.0175	0.0029	0.00026	0
Windmill Point	14	1	0.0023	−4.84	0.462	0.0087	0.0068	0.0113	0.0154	0.00880	−0.00041

[a]Outlier deleted.
[b]2,3,3′,4,4′,5′,6′-heptachlorobiphenyl.
[c]Missing sample.

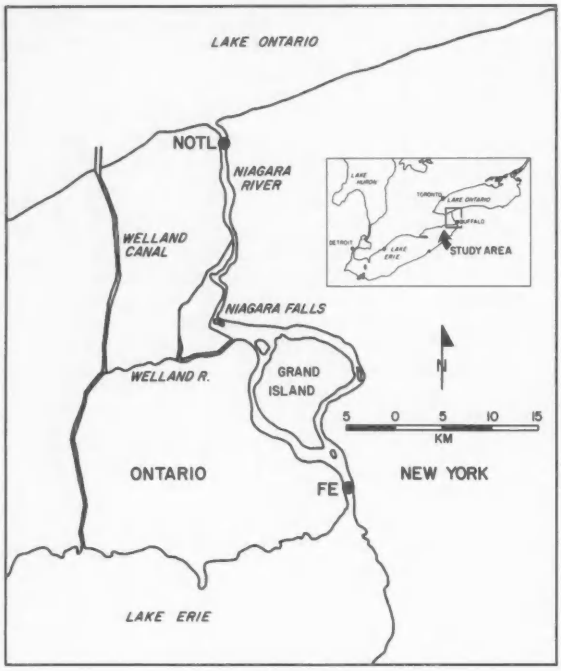

FIG. 1. Niagara River.

chosen to reflect the ability of the method in dealing with different censoring levels and to cover areas in the Great Lakes which are of major concern.

In Table 1 the number of samples N, the number of samples below the detection limit n_0, the detection limit X_0; the MLE of μ, σ, α, the confidence limits for $\hat{\alpha}$, and the elements of the variance–covariance matrix for $\hat{\mu}$ and $\hat{\sigma}$ are given.

1. Niagara River

The Niagara River Toxics Committee (NRTC), a binational group of representatives from Environment Canada, Ontario Ministry of the Environment, the U.S Environmental Protection Agency, and the New York Department of Environmental Conservation, established an ambient large volume water and suspended sediment monitoring program. One of the objectives of the monitoring was "to estimate the relative differences in the loadings of chemicals of concern between the river's source and mouth." A joint evaluation of upstream/downstream Niagara River monitoring data(1984–1986), was prepared by the Data Interpretation Group of the NRTC. The background information for this program can be found in that report.

Substantial percentages of the data from this program were reported as below the detection limit. In the joint evaluation report, the LR method of Gilliom and Helsel (1986) was applied to the data to allow estimation of mean concentrations for the head (Fort Erie) and mouth (Niagara-on-the-Lake) of the Niagara River and (Fig. 1) for estimation of differential loading between these two points.

Table 1 contains the results of the MLE method applied to the alpha and gamma chlordane data from this program. Although the number of values reported below the detection limit is large (n_0) compared with the sample size (N) it is still possible to estimate a mean concentration (α). However, the approximate 95% confidence interval for the ratio of downstream concentration to upstream concentration for alpha-chlordane (0.611, 2.55) and gamma-chlordane (0.0288, 2.03) both include 1.0, so the differences between sites is not significant for either chemical.

2. Lake Ontario

In 1981, Kaiser et al. (1983) sampled volatile halocarbons in the Niagara River and Lake Ontario (Fig. 2). They reported the

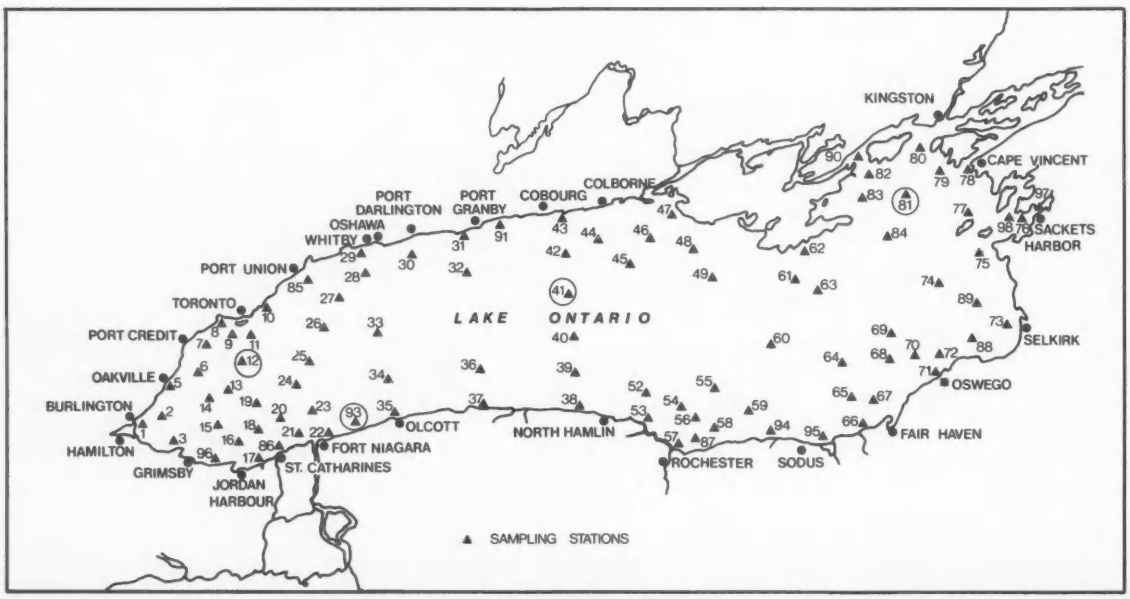

FIG. 2. Sampling stations in Lake Ontario.

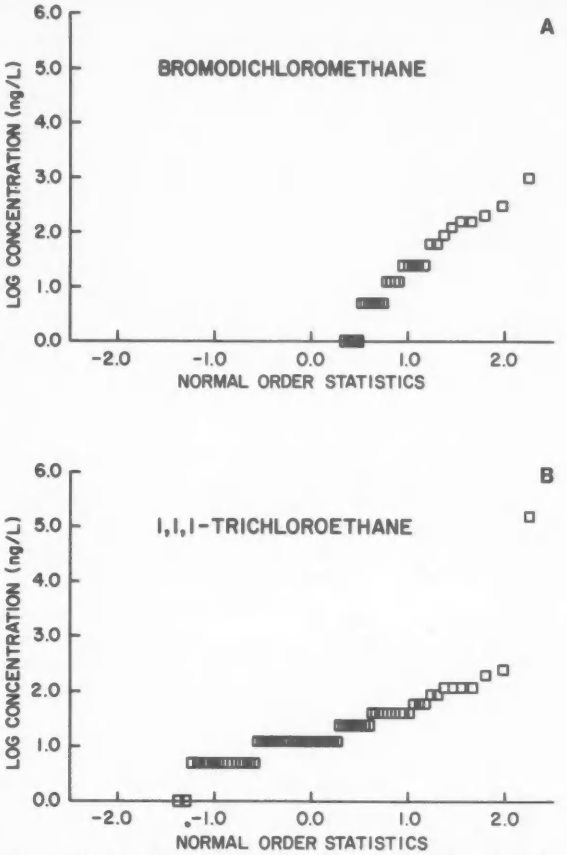

FIG. 3. (A) Distributional plot for biomodichloromethane in Lake Ontario, 1981; (B) Distributional plot for 1,1,1-Trichloroethane in Lake Ontario, 1981.

lake-wide mean and standard deviation for bromodichloromethane as 1.9 and 3.2 ng·L^{-1}, respectively and for 1,1,1-trichloroethane as "trace levels or absent." Table 1 contains the results of using the MLE procedure to estimate the means. For both chemicals, a lognormal distribution of the data was assumed (Fig. 3). The estimated mean for 1,1,1-trichloroethane is ≈3.8 ng·L^{-1} with a 95% confidence interval of (3.2, 4.6). This estimate excludes one value of 180 ng·L^{-1} which was identified as an outlier. The estimated mean for bromodichloromethane is ≈3.2 ng·L^{-1} with a 95% confidence interval of (1.1, 14.6). The substantially larger confidence interval is due to the large number of less than values reported (52 of 82 samples) and to a few high values (12 and 20 ng·L^{-1}) which were not identified as outliers.

3. Detroit River

The Modeling Committee of the Upper Great Lakes Connecting Channels Study has attempted to perform a mass balance on the Detroit River (Fig. 4) using samples taken at the head (at Windmill Point) and the mouth (at Grosse Ile). Sampling was conducted for many conservative, nutrient, metal, and organic parameters twice a day for a 1-wk period during the spring and summer. Samples were taken by integrating each transect according to the horizontal flow distribution in the river

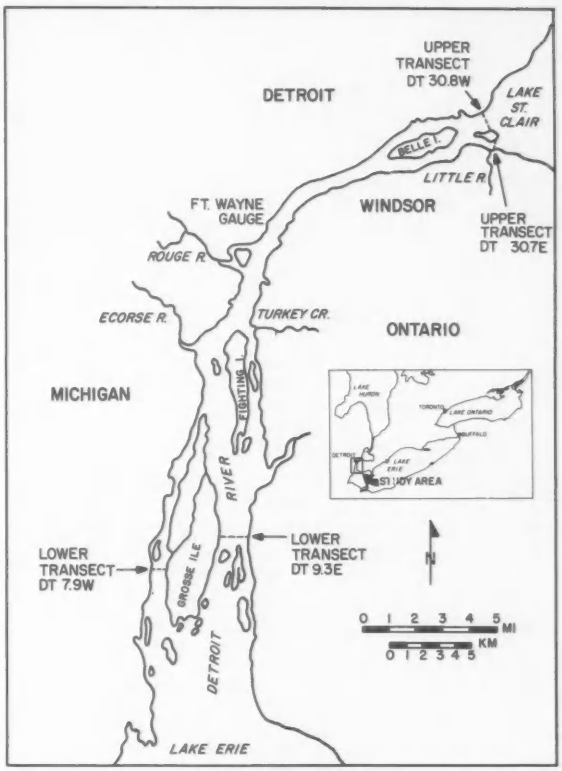

FIG. 4. Detroit River.

at that point. Upstream and downstream sampling times were lagged by 18 h to account for time of travel in the river.

Because many of the chemicals were measured in trace amounts, certain percentages of the data were reported as ND (nondetectable or below the detection limit). Without a consistent and unbiased way of handling these measurements, the task of estimating loadings for these chemicals and associated confidence intervals would be extremely difficult.

In the case of total phosphorus, the one less than value causes difficulties when pairing the data for difference calculations. It also does not allow conventional confidence limits to be estimated. For PCB congener 191 (Windmill Point) 8 of 13 values were found to be below the detection limit (3.0 pg·L^{-1}) upstream of the major sources. However, it is necessary to define a background level against which to compare the downstream load to obtain a difference.

The results are presented in Table 1. The approximate 95% confidence interval for the ratio of downstream to upstream concentrations are (1.36, 2.37) for total phosphorus and (1.58, 4.94) for PCB 191. For both substances the calculations indicate that a significant increase occurs over the length of the Detroit River. The estimation of confidence intervals is feasible and the results are intuitively reasonable.

Discussion

The example applications summarized in Table 1 raise questions concerning the effect of changing the detection limit. Sometimes a lab will be uncomfortable with reporting very low

TABLE 2. Summary of results for effect of changing detection limits (X_0).

	Detection limit							Confidence interval	
	X_0	$\hat{\mu}$	$\hat{\sigma}$	V_{11}	V_{22}	V_{12}	$\hat{\alpha}$	Lower	Upper
Lake Ontario									
1,1,1-Trichloroethane(ng·L^{-1})	0.1	0.9510	1.1014	0.01517	0.00879	−0.00044	4.747	3.485	6.467
N = 81 n_0=6	0.2	1.0035	0.9329	0.01088	0.00628	−0.00031	4.215	3.296	5.391
	0.3	1.0340	0.8390	0.00880	0.00506	−0.00025	3.999	3.228	4.953
	0.4	1.0554	0.7754	0.00752	0.00431	−0.00022	3.881	3.197	4.711
	0.5	1.0720	0.7282	0.00663	0.00379	−0.00019	3.808	3.183	4.556
	0.6	1.0854	0.6914	0.00598	0.00340	−0.00017	3.760	3.178	4.449
	0.7	1.0967	0.6616	0.00547	0.00310	−0.00016	3.727	3.177	4.371
	0.8	1.1064	0.6369	0.00507	0.00287	−0.00014	3.703	3.180	4.313
	0.9	1.1149	0.6161	0.00475	0.00268	−0.00013	3.687	3.184	4.269
LR method	—	1.2486	0.2434	—	—	—	5.965		

detection limits and will therefore choose a conservative value that applies to even the worst case. Another possibility is that the detection limit can actually change during the time it takes for a set of samples to be analyzed. This is a strong possibility for organic chemicals determined by chromatography, because the detection limit is affected by the baseline drift which varies from run to run. Table 2 presents the effects of varying the detection limit on the estimates of the parameters using the 1,1,1-trichloroethane data in Lake Ontario. The effect of changing the detection limit from 0.1 to 0.9 ng·L^{-1} (lowest reported value was 1 ng·L^{-1}) in increments of 0.1 ng·L^{-1} was to increase $\hat{\mu}$ but to decrease $\hat{\sigma}$ thereby decreasing $\hat{\alpha}$ and shrinking the confidence interval. This is intuitively reasonable since a detection limit far from the lowest reported value results in the left tail of the distribution of concentrations (or their logs) having a larger weight in the estimation of the mean. This implies that values should be reported as close as possible to the detection limit.

Table 2 also includes the LR estimate for 1,1,1-trichloroethane. This method does not take into account the actual value of the detection limit. The application of this method results in an estimated mean lake-wide concentration of ≃6.0 ng·L^{-1} which is higher than the upper limit of the confidence interval for all of the results in Table 2 except for X_0 = 0.1 ng·L^{-1}.

The method of maximum likelihood estimation is not new, but its application to censored data has always been difficult. With the approximation of Tiku (1967) now applied to Type I censored data in this paper the method can be used routinely without the disadvantage of computational difficulty which was previously the case. Several example applications of the MLE method to water quality data have illustrated the utility of it in solving basic questions of interest in environmental science.

Acknowledgements

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Appendix

The actual calculations leading to the estimates in Table 1 are presented in a step by step manner for the case of total phosphorus in the Detroit River at Windmill Point. The smallest data set was chosen for illustrative purposes. Example calculation, phosphorus in Detroit River; Upstream, (Windmill Point)

Data (mg·L^{-1}): 0.0146, 0.0116, 0.0113, 0.0109, 0.0107, 0.0097, 0.0083, 0.0083, 0.0069, 0.0069, 0.0064, 0.0064, 0.0063, ND.

Detection limit = 0.0023 mg·L^{-1}, sample size = N = 14, No. of nondetects = n_0 = 1, No. of detects = n = 13, h = n_0/n = 0.07692.

1. Take natural logs of all concentration data including detection limit and find, in log space:

$$\bar{y} = -4.736$$
$$s^2 = 0.0714$$
$$y_0 = -6.075$$

2. Now find β_0 and β_1 as per Tiku (1967)

with $p = n_0/N = 1/14 = 0.07143$,

$$a = \Phi^{-1}\left[p - \sqrt{p(1-p)/N}\right] = \Phi^{-1}[0.07143 - \sqrt{(0.07143)(0.92857)/14}]$$
$$= \Phi^{-1}[0.00260]$$
$$= -2.7946$$

$$b = \Phi^{-1}\left[p + \sqrt{p(1-p)/N}\right] = \Phi^{-1}[0.07143 - \sqrt{(0.07143)(0.92857)/14}]$$
$$= \Phi^{-1}[0.14026]$$
$$= -1.0792$$

$$g(a) = \frac{e^{-a^2/2}}{\sqrt{2\pi}\,\Phi(a)} = \frac{e^{-(-2.7946)^2/2}}{\sqrt{2\pi}\cdot\Phi(-2.7946)}$$
$$= 3.09225$$

$$g(b) = \frac{e^{-b^2/2}}{\sqrt{2\pi}\,\Phi(b)} = \frac{e^{-(-1.0792)^2/2}}{\sqrt{2\pi}\cdot\Phi(-1.0792)}$$
$$= 1.58857$$

$$\beta_1 = \frac{(g(b) - g(a))}{b - a} = \frac{(1.58857 - 3.09225)}{-1.0792 - -2.7946}$$
$$= -0.87656$$

$$\beta_0 = g(a) - a\cdot\beta_1 = 3.09225 - (-2.7946)(-0.87656)$$
$$= 0.64263.$$

3. The maximum likelihood estimates are $\hat{\mu}$ and $\hat{\sigma}$ in

$$\hat{\mu} = \frac{\bar{y} - h\beta_1 y_0 - h\beta_0\hat{\sigma}}{1 - h\beta_1}$$

and $\hat{\sigma}$ is the positive root of the quadratic equation

$$\hat{\sigma}^2 - s^2 - (\bar{y} - \hat{\mu})^2 + h\xi(\beta_0 + \beta_1\xi)\hat{\sigma}^2 = 0,$$

which yield $\hat{\mu} = -4.84$ and $\hat{\sigma} = 0.462$ after iterative solution.

The variance–covariance matrix is:

$$V = \frac{(0.462)^2}{13}\left[1 - 0.07692(-0.87656)\right.$$
$$\left.\frac{2(-4.736 - (-4.84))}{0.462} - 0.07692(0.64263 + 2(-0.87656)(-2.6699))\right.$$
$$\left.\frac{2(-4.736 - (-4.84))}{0.462} - 0.07692(0.64263 + 2(-0.87656)(-2.6699))\right.$$
$$\left.\frac{3((0.267)^2 + (-4.736 - (-4.84))^2)}{(0.462)^2} - 1 - 0.07692(-2.6699)\right]^{-1}$$
$$(3(-0.87656)(-2.6699) + 2(0.64263))$$

$$= \begin{bmatrix} 0.0154 & -0.00041 \\ -0.00041 & 0.0088 \end{bmatrix}$$

4. Back transform to observation space:

$$\hat{\alpha} = e^{\hat{\mu} + 1/2\,\hat{\sigma}^2} = e^{(-4.84 + (0.462)^2/2)}$$
$$= 0.00878$$

Find

$$Q = V_{11} + 2V_{12}\hat{\sigma} + \hat{\sigma}^2 V_{22}$$
$$= 0.0154 + 2(-0.00041)(0.462) + (0.462)^2(0.0088)$$
$$= 0.0169,$$

α (unbiased)

$$= \hat{\alpha}\left[e^{-Q/2}\right] = 0.00878\left[e^{-0.0169/2}\right]$$
$$= 0.0087$$

Approximate 95% C.I.:

$$0.00878\, e^{-1.96\sqrt{0.0169}} \text{ and } 0.00878 e^{1.96\sqrt{0.0169}}$$
$$= (0.0068, 0.0113)\ \text{mg}\cdot\text{L}^{-1}.$$

Mercury in Crayfish Species from Thirteen Ontario Lakes in Relation to Water Chemistry and Smallmouth Bass (*Micropterus dolomieui*) Mercury

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Allard, M., and P. M. Stokes. 1989. Mercury in crayfish species from thirteen Ontario lakes in relation to water chemistry and smallmouth bass (*Micropterus dolomieui*) mercury. Can. J. Fish. Aquat. Sci. 46: 1040–1046.

Total mercury was determined in crayfish from 13 lakes in South-Central Ontario that receive no direct discharge of mercury to their watersheds. Mercury concentration in crayfish abdominal muscles ranged from 0.022 to 0.614 $\mu g \cdot g^{-1}$ wet weight and was positively related with weight in *Cambarus bartoni*, *C. robustus*, *Orconectes obscurus*, *O. propinquus*, and *O. virilis*. Bioaccumulation of mercury in the early maturing and comparatively small body-sized *O. propinquus* was faster than in any other species. There were significant differences in mercury concentrations in crayfish among the lakes. Conductivity of lake water alone explained 54% of the variability observed among lakes for mercury in abdominal muscle of a 10-g crayfish. Moreover, mercury levels in *C. bartoni* and *C. robustus* were significantly higher in lake inlets than in the corresponding lake basin. Mercury in smallmouth bass was also positively correlated with crayfish mercury. From these results, we conclude that high mercury concentrations in biota were related to low mineralization of lake or inlet water and to the sensitivity to acidification. We also recommend that crayfish be used as biomonitors of mercury in addition to proving useful toward a better understanding of mercury pathways in these remote lakes.

Nous avons analysé le mercure total dans les écrevisses de 13 lacs du centre-sud de l'Ontario dont aucun ne recevait d'apport direct de mercure dans leur bassin de drainage. Les concentrations de mercure dans le muscle abdominal des écrevisses variaient de 0.021 à 0.614 $\mu g \cdot g^{-1}$ de poids frais et étaient corrélées positivement avec le poids total chez *Cambarus bartoni*, *C. robustus*, *Orconectes obscurus*, *O. propinquus*, et *O. virilis*. La bioaccumulation du mercure était plus rapide pour *O. propinquus*, l'espèce la plus petite dont la maturité est précoce, que pour toutes les autres espèces d'écrevisses. Les concentrations de mercure dans les écrevisses différaient significativement entre les lacs. Les valeurs de conductivité de l'eau expliquaient, à elles seules, 54% de la variabilité entre pour les lacs concentrations de mercure prédites dans le muscle abdominal d'une écrevisse de 10g. Les concentrations en mercure chez *C. bartoni* et *C. robustus* étaient significativement plus élevées pour les écrevisse prélevées dans les tributaires plutôt que dans le lac du même bassin. Les concentrations de Hg dans l'achigan à petite bouche étaient corrélées de façon positive avec les concentrations de mercure dans les écrevisses. D'après nos résultats, nous concluons que les fortes concentrations de mercure dans le biota sont liées à la faible minéralisation des eaux qui rend celles-ci plus facilement acidifiables. Nous recommendons l'utilisation d'écrevisses comme bioindicateur de la présence de mercure et comme matériel pour étudier le cheminement de ce métal dans les lacs qui ne sont pas directement pollués.

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In Canada, high mercury (Hg) concentrations have been observed in biota from rivers and lakes polluted by discharges of this metal into the ecosystem (Rudd et al. 1983; Rada et al. 1986), and in recently flooded areas, especially reservoirs (Bodaly et al. 1984; Stokes and Wren 1987). Fish in lakes remote from point sources of Hg and in lakes that have not been flooded have also been shown to have elevated Hg concentrations. Mercury contents in such fishes, especially in older individuals of predatory species, often exceeds the federal guidelines (0.5 $\mu g \cdot g^{-1}$) for unrestricted consumption (Suns et al. 1987; Wren and MacCrimmon 1983). Although we know that fish can absorb Hg directly from the water across the gill membranes as well as from its food (Norstrom et al. 1976; Mathers and Johansen 1985), we still need to determine the source of this Hg and the factors that promote its bioaccumulation in lakes with no known point source.

Crayfish could be a potential source of Hg since they serve as food for fish and wildlife. For instance, crayfish constitute more than 60% of the diet of smallmouth bass (*Micropterus dolomieui*) (Fedoruk 1966; Stein 1977). Mink and otter which rely partly on aquatic organisms including crayfish for food, had Hg concentrations higher than 1 ppm in liver and kidney in Muskoka Region lakes (Wren et al. 1986). Crayfish have also been shown to accumulate Hg in their tissues and to be good biomonitors of Hg pollution in aquatic systems (Vermeer 1972; Sheffy 1978; Rada et al. 1986). Finally, since the activity

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range of crayfish is more restricted compared with that of fish, crayfish could prove useful in detecting areas within watersheds where Hg bioavailability is high.

The purpose of our study was to examine Hg levels in crayfish inhabiting lakes remote from point sources of Hg in order to bring new knowledge on bioaccumulation processes. We sought answers to three specific questions: (1) Is there a relationship between crayfish and smallmouth bass Hg? Since smallmouth bass are feeding on crayfish, and if we assume that part of fish Hg might come from its alimentation, we would normally expect a relationship between crayfish and fish Hg. To answer this question, we also ought to check whether crayfish Hg is related to crayfish size (weight); if it is the case, comparisons between fish and crayfish Hg should be done using Hg concentrations in hypothetical organisms of a given size. (2) Are bioaccumulation patterns different among crayfish species? Fish species do not bioaccumulate Hg to the same extent or at the same rate. Differences in Hg bioaccumulation if fish are usually linked with differences in ecology, in life cycles, or in trophic status (Mathers and Johansen 1985). Although most crayfish species are classified as omnivorous, there is among them major differences in life cycle or in ecology (Hamr and Berrill 1985). Therefore, we might expect differences in bioaccumulation pattern among them. (3) Is there a relationship between crayfish Hg and the water chemistry or the morphometry of the lake? In previous work, water chemistry or lake morphometry explained in part the among lake variability found in fish Hg. If processes are the same for both fish and crayfish, we should expect that the same environmental factors will also influence crayfish Hg.

Materials and Methods

Study Area

Thirteen lakes, located in the Administrative Region 50 (Algonquin Region) of the Ontario Ministry of Natural Resources (MNR), were sampled for crayfish (Table 1). The lakes showed a gradient of Hg concentrations in smallmouth bass; with the exception of Peninsula and Vernon, all lakes had Hg data for at least 15 smallmouth bass (Table 2). Peninsula and Vernon were included in the study because of the extensive Hg survey done by the Ontario Ministry of Environment (MOE) in their watersheds (G. Mierle, Dorset Research Centre, P.O. Box 39, Bellwood Acres Rd., Dorest, Ontario P0A 1E0, pers. comm.).

Eleven of the lakes are located on the Canadian Precambrian Shield characterized by granitic rocks providing very low buffering to the surface waters. Alkalinities in these lakes were usually below 10 $mg \cdot L^{-1}$. The remaining two, Four Mile and Gull, are located at the border of the shield and sit on sedimentary rocks rich in limestone and as a result have higher alkalinities (Table 2).

The morphometry, water chemistry, and fish data of the study lakes were obtained from the MNR and MOE (Refer to McMurtry 1987, for details regarding the sampling and data analysis).

Crayfish Collection

Crayfish were collected between 1 June and 30 August 1986. Each of the study lakes was surveyed twice, during the first half and the second half of the period, respectively. Crayfish were collected by hand from the shoreline of the lake, by snorkelling in shallow waters, and with minnow traps baited with fish remains or (rarely) beef liver. In two of the lakes (Little Hawk and Lake Vernon), streams (inlets) were searched by hand in order to make comparisons between lake and stream crayfish. Time limitation did not permit to search for stream crayfish in all the studied watersheds. After collection, crayfish were brought to the lab in a cooler, and frozen immediately upon arrival. Later they were thawed, and identified to species according to Crocker and Barr (1968). Crayfish length (CPL) was measured from the rostral tip to the posteriomedian end of the cephalothorax with a vernier caliper, and the crayfish were weighed on a pesola scale to the nearest 0.1 g. Crayfish were dissected and the abdominal muscle (without the exoskeleton) was removed and frozen until Hg determination. Crayfish abdominal muscle was selected because of its capacity to accumulate more Hg than any other tissue (Vermeer 1972; Armstrong and Hamilton 1973; Stinson and Eaton 1983).

Mercury Analysis

The frozen abdominal muscles were thawed, and approximately 180 mg were removed and digested in 2 mL of 4:1 sul-

TABLE 1. Morphometric characteristics of lake sampled[1].

Lake	County	Latitude	Longitude	Lake area (ha)	Depth (m)		Elevation (m)	Morphoedaphic index (m)	Secchi (m)
					Maximum	Mean			
Bear	Haliburton	45°20′N	78°42′W	94.8	36.6	9.4	355	2.7	7.9
Dickie	Muskoka	45°09′N	79°05′W	91.1	12.2	4.9	366	4.5	2.9
Four Mile	Victoria	44°41′N	78°45°W	786.8	19.2	8.5	270	15.8	4.3
Galeairy	Nipissing	45°30′N	78°17′W	7.5	n.a.[2]	n.a.[2]	n.a.[2]	n.a.[2]	n.a.[2]
Gull	Haliburton	44°51′N	78°47′W	995.8	49.1	16.5	270	2.5	5.8
Kimball	Haliburton	45°21′N	78°41′W	212.6	67.1	22.5	358	1.1	9.1
Little Hawk	Haliburton	45°09′N	78°43′W	342.8	86.9	30.7	360	0.7	6.9
Opeongo	Nipissing	45°42′N	78°23′W	5158.1	49.4	14.6	404	1.8	5.5
Peninsula	Muskoka	45°20′N	79°07′W	865.4	34.1	9.0	283	n.a.[2]	n.a.[2]
Rebecca	Muskoka	45°26′N	79°02′W	210.7	29.0	7.9	356	3.3	4.7
Round	Parry Sound	45°28′N	79°24′W	190.4	21.4	6.7	305	3.5	2.8
Lake Vernon	Muskoka	45°20′N	79°17′W	1443.1	37.1	12.7	283	n.a.[2]	n.a.[2]
Waseosa	Muskoka	45°24′N	79°17′W	156.7	19.2	6.5	333	3.3	3.0

[1]Data obtained from the merged mercury dataset compiled from the MOE/MNR mercury in sport fish, MNR lake inventory, and MNR sensitivity data sets (McMurtry 1987).

[2]Data not available.

TABLE 2. Water chemistry and mercury concentrations in smallmouth bass in the study lakes[1].

Lake	pH	Alkalinity ($mg \cdot L^{-1}$)	Conductivity ($\mu S \cdot cm^{-1}$)	DOC	Ca	Mg	Na ($mg \cdot L^{-1}$)	K	SO_4	Smallmouth bass Hg ($\mu g \cdot g^{-1}$) (n)	Mean	(Range)
Bear	6.6	3.81	29.7	3.8	2.78	0.86	0.82	0.44	6.50	(18)	0.48	(0.28–0.99)
Dickie	6.0	1.26	26.0	3.9	2.10	0.48	0.70	0.46	6.27	(22)	0.72	(0.18–1.73)
Four Mile	7.8	90.7	191.0	4.7	32.0	4.48	1.35	0.50	8.58	(20)	0.30	(0.08–0.90)
Galeairy	6.4	3.63	36.0	4.4	2.90	0.78	1.05	0.56	7.70	(16)	0.41	(0.28–0.70)
Gull	7.5	23.74	74.9	3.4	9.96	1.88	1.50	0.80	8.22	(25)	0.48	(0.11–1.63)
Kimball	6.3	1.49	30.0	2.3	2.70	0.68	0.55	0.38	8.50	(29)	0.72	(0.39–1.70)
Little Hawk	6.6	3.81	28.2	2.4	2.65	0.74	0.59	0.44	7.30	(40)	0.51	(0.10–0.99)
Opeongo	6.5	4.30	42.5	3.4	3.30	1.20	1.10	0.64	8.80	(21)	0.26	(0.11–1.20)
Peninsula	6.9	7.15	56.0	n.a.[2]	4.60	n.a.[2]	n.a.[2]	n.a.[2]	n.a.[2]	(n.a.[2])	n.a.[2]	(n.a.[2])
Rebecca	7.0	5.32	33.3	3.7	3.51	0.84	0.91	0.58	6.64	(20)	0.64	(0.39–0.96)
Round	6.4	3.47	26.0	5.5	2.81	0.63	0.74	0.42	5.34	(23)	1.29	(0.25–2.89)
Lake Vernon	n.a.[2]	n.a.[2]	n.a.[2]	n.a.[2]	n.a.[2]	n.a.[2]	n.a.[2]	n.a.[2]	n.a.[2]	(9)	1.56	(0.72–2.87)
Waseosa	7.0	4.67	32.6	3.8	3.34	0.79	0.97	0.51	6.46	(16)	0.88	(0.20–2.40)

[1]Data obtained from the merged mercury dataset compiled from the MOE/MNR mercury in sport fish, MNR lake inventory, and MNR sensitivity data sets (McMurtry 1987). (Water chemistry was done on tube composite sample taken at deepest depth in the lake, in fall).
[2]Data not available.

TABLE 3. Correlations between the predicted mercury concentration (log_{10}Hg) of a hypothetical 10-g crayfish and lake variables $n = 10$ lakes, $*P<0.05$, $**P<0.01$.

Lake variables	Variable transformation	r
Lake area	Log_{10}	−0.544
Maximum depth	none	−0.181
Mean depth	none	−0.277
Elevation	none	0.518
Morphoedaphic index	Log_{10}	−0.217
Secchi	Log_{10}	−0.146
pH	none	−0.630*
Alkalinity	Log_{10}	−0.713*
Conductivity	Log_{10}	−0.771**
DOC	none	0.113
Ca	Log_{10}	−0.751**
Mg	Log_{10}	−0.731*
Na	none	−0.715*
K	none	−0.620*
SO_4	none	−0.634*
Smallmouth bass (31 cm) Hg	Log_{10}	0.621*

phuric–nitric acid mxture at 230°C for 12–16 h (MOE 1983). The cooling solution was diluted to 10 mL with distilled water and analyzed for total Hg by cold vapour atomic absorption spectrophotometry using a Pharmacia mercury monitor (Model 100-M). Duplicates, spiked samples, and standard oyster tissues (U.S. National Bureau of Standards No. 1566, certified 0.057 $\mu g\ Hg \cdot g^{-1}$) were run every 10 to 15 samples. Detection limit, accuracy, and precision were respectively 0.01 $\mu g \cdot g^{-1}$, 1.6, and 6%. Mean recovery rate of spiked samples was 102%. All results are reported as micrograms Hg per gram fresh weight.

Data Analysis

For any given species in a lake, data from all sites and for both sex were pooled. Lake and inlet sites were, however, evaluated separately. All Hg concentrations were transformed to log_{10} in order to normalize the data. Simple linear regressions were estimated whenever possible using transformed Hg data as the dependent variable against the total weight of the crayfish. This latter variable did not need transformation to satisfy the requirement of the analysis. The crayfish weight was selected instead of its length, because we wished to compare the different crayfish species; and we were concerned about differing weight–size relationships among the species.

Comparisons between pairs of species within a lake and comparisons among lakes for the same species were done using Student's t-test or analysis of covariance.

Mercury concentrations in crayfish were correlated with fish concentrations and with lake variables. Predicted Hg for a 10-g hypothetical crayfish (from our previous regression analysis) and for a 31-cm hypothetical fish (calculated from the regression of Hg over total length of fish in McMurtry 1987) were used in the correlations. Only the lakes from which a predicted Hg value could be calculated for both crayfish and fish (Bear, Dickie, Four Mile, Gull, Kimball, Little Hawk, Opeongo, Rebecca, Round, and Waseosa) were included in the analysis. Some of the variables were transformed to satisfy the requirement of homogeneity of variance and normality; in all cases, a logarithmic transformation proved satisfactory (Table 3).

The predicted Hg concentrations in crayfish were regressed against sets of environmental variables. Variables were divided in two sets (morphometry and chemistry), since the number of lakes was too small to include all independent variables in a single run. Stepwise multiple regressions were run for predicted Hg in crayfish (10 g) and a selected set of independant morphometric variables (lake area, elevation, morphoedaphic index, and secchi depth). Independent water chemistry variables were regressed separately (using conductivity, dissolved organic carbon and potassium). No other variables were included in the analysis because they were highly correlated with those mentioned above. Variables selected in each of the multiple regression runs were then run together.

Results

Mercury Concentrations in Crayfish Abdominal Muscle

Seven crayfish species were collected, and mercury was determined in 618 abdominal muscles samples. Mercury concentrations in abdominal muscles ranged from 0.021 to 0.614 $\mu g \cdot g^{-1}$, while crayfish weight ranged from 0.4 g to 35.0 g. Results were retained for further analysis, only when more

TABLE 4. Mean and range of mercury concentrations and crayfish total weight, for each crayfish species and each lake. Hg–Weight regression equations are given only when the relationship is significant (*$P<0.05$, **$P<0.01$, ***$P<0.001$). Within each species, regression equations that are followed by the same letter are not significantly different. (L) = collected in lake; (S) = collected in inlet.

Species	Lake	Hg–Weight (wt) regressions	r	n	Hg ($\mu g \cdot g^{-1}$) Mean	SD	(Range)	Weight (g) Mean	SD	(Range)
C. bartoni	Bear	Log Hg = 0.031 WT − 1.16a*	0.379	39	0.124	0.044	(0.032–0.243)	7.1	2.2	(2.3–11.7)
	Kimball	Log Hg = 0.062 WT − 1.57b***	0.861	43	0.089	0.057	(0.031–0.243)	7.3	3.5	(1.9–14.6)
	Little Hawk (L)	Log Hg = 0.039 WT − 1.46b*	0.566	16	0.073	0.038	(0.035–0.183)	7.1	2.8	(2.6–13.3)
	Little Hawk (S)			6	0.197	0.101	(0.075–0.383)	2.9	1.6	(0.90–4.6)
	Opeongo	Log Hg = 0.028 WT − 1.29b*	0.413	31	0.077	0.043	(0.033–0.276)	4.5	2.2	(1.3–10.1)
	Peninsula	Log Hg = 0.054 WT − 1.48b***	0.596	40	0.069	0.030	(0.025–0.191)	5.4	1.8	(1.7–10.2)
	Rebecca	Log Hg = 0.049 WT − 1.39b***	0.732	33	0.145	0.070	(0.029–0.304)	10.0	4.0	(2.5–17.8)
	Round	Log Hg = 0.052 WT − 1.37b***	0.684	35	0.081	0.047	(0.038–0.243)	4.5	2.5	(1.0–13.0)
	Lake Vernon (L)	Log Hg = 0.034 WT − 1.04c***	0.588	30	0.227	0.102	(0.090–0.488)	10.2	3.4	(1.8–16.5)
	Lake Vernon (S)	Log Hg = 0.019 WT − 0.62d*	0.717	8	0.304	0.073	(0.199–0.449)	4.9	3.8	(1.7–12.0)
C. robustus	Dickie	Log Hg = 0.015 WT − 1.16a**	0.534	19	0.087	0.033	(0.044–0.155)	4.9	5.5	(0.4–20.0)
	Gull	Log Hg = 0.018 WT − 1.56b***	0.763	22	0.062	0.036	(0.028–0.146)	16.8	9.7	(1.8–35.0)
	Little Hawk (L)			16	0.072	0.020	(0.044–0.115)	8.7	3.5	(1.5–16.3)
	Little Hawk (S)			8	0.123	0.020	(0.099–0.159)	2.7	3.1	(0.9–10.2)
C. obscurus	Galeairy	Log Hg = 0.039 WT − 1.34**	0.469	31	0.073	0.029	(0.022–0.166)	4.4	2.3	(1.2–10.5)
O. propinquus	Four Mile	Log Hg = 0.094 WT − 1.67a***	0.661	27	0.042	0.018	(0.015–0.115)	2.8	1.1	(1.6–7.5)
	Waseosa	Log Hg = 0.087 WT − 1.28b**	0.483	34	0.095	0.052	(0.035–0.338)	2.5	1.0	(1.0–4.8)
O. virilis	Bear			24						
	Four Mile	Log Hg = 0.024 WT − 1.50a***	0.789	14	0.095	0.025	(0.063–0.168)	4.9	2.3	(2.3–10.5)
	Rebecca	Log Hg = 0.032 WT − 1.39b***	0.680	27	0.059	0.035	(0.028–0.165)	9.3	6.5	(2.1–23.3)
	Waseosa	Log Hg = 0.037 WT − 1.24c***	0.538	23	0.082	0.034	(0.030–0.176)	8.6	3.9	(2.3–18.0)
					0.083	0.036	(0.042–0.183)	3.4	2.3	(1.4–11.5)

than 10 individuals of any given species were collected in the same lake. Mean Hg concentrations, mean crayfish total weight, ranges and Hg–weight regressions when significant are presented for five crayfish species, *Cambarus bartoni, C. robustus, Orconectes obscurus, O. propinquus*, and *O. virilis* (Table 4). Significant, positive correlations between Hg concentration and weight were found in all five species in almost every lake for which we had data. In two instances in Bear and Little Hawk lakes, there was no relationship between Hg and crayfish weight. Such results could be expected if most of the collected crayfish are of the same age class, however, we do not know whether this was the case here.

Comparison between Species

Bioaccumulation of Hg considered here as the increase in Hg concentrations with crayfish weight in different species was compared whenever we had data for more than one species in a lake. Regression lines (slope and intercept) were compared when a Hg–size relationship was established.

C. bartoni and *O. virilis*: Bioaccumulation of Hg was not significantly different between these two species, i.e. there was no significant difference in the slope and intercept of the regression lines of these two species in Rebecca Lake (Table 4).

O. virilis and *O. propinquus*: In Four Mile and Waseosa lakes, the slope of the regression was significantly greater ($P<0.05$) in *propinquus* (Table 4).

In general, the slope of the Hg–size regressions was highest for *O. propinquus* and lowest for *C. robustus*, while the slopes of *C. bartoni* and *O. virilis* were intermediate (Table 4).

Comparisons between Inlet and Lake Crayfish

Cambarus bartoni was collected from both inlet and lake sites in Little Hawk and Vernon. In Vernon, crayfish collected in the inlet contained significantly more Hg ($P<0.05$) than those collected in the lake basin itself. In Little Hawk, crayfish collected in one of the inlet were of very low weight (<5g) and no regression line could be established. However, Hg concentrations in the inlet crayfish were more than five times greater than the Hg concentrations in lake crayfish of the same weight (Table 4).

Cambarus robustus collected in Little Hawk inlet contained significantly more Hg than those collected in the lake although the inlet crayfish were significantly smaller ($P<0.05$) (Table 4).

Crayfish Hg, Fish Hg, Physical and Chemical Factors

Pooled species/lake data showed that crayfish Hg was inversely correlated ($P<0.05$) with most of the water chemistry variables with the only exception of dissolved organic carbon (DOC). DOC and all the morphometric variables were not correlated with crayfish Hg (Table 3). Fish Hg was positively correlated with crayfish Hg (Fig. 1).

Elevation and lake area taken altogether explained 52% of the variance in predicted Hg in crayfish (Table 5). Only one variable, conductivity, was selected in the multiple regression of predicted crayfish Hg over the subset of water chemistry variables; conductivity explained 54% of the variance in predicted crayfish Hg (Table 6).

When the selected morphometric and water chemistry variables were run together, only conductivity remained significant, as elevation and lake area were correlated with conductivity. The relationship between predicted crayfish Hg and conductivity is presented in Fig. 2.

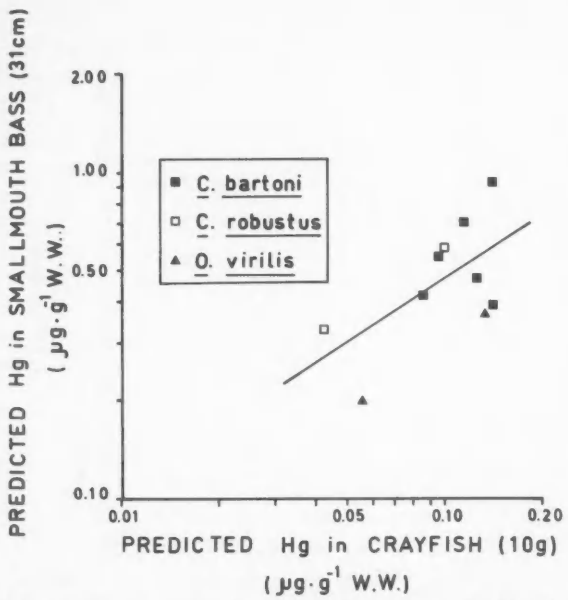

FIG. 1. Predicted mercury in smallmouth bass at a standard length (31 cm) in relation to the predicted mercury in crayfish abdominal muscle at a standard total weight (10 g) in 10 of our study lakes (Bear, Dickie, Four Mile, Gull, Kimball, Little Hawk, Opeongo, Rebecca, Round, and Waseosa). A significant positive relationship was observed between predicted mercury in fish and predicted mercury in crayfish, where:

$$\text{Log Hg}_{\text{fish}} = 0.644 \text{ Log Hg}_{\text{cfish}} + 0.319,\ r=0.621,\ P<0.05.$$

TABLE 5. Variables selection in stepwise multiple regression of predicted mercury concentration in a hypothetical 10-g crayfish $\log_{10}$(Hg) on lake surface ($\log_{10}$), elevation, and morphoedaphic index ($\log_{10}$).

Variable	Slope	Cumulative R^2	F	P
Elevation	0.0024	0.255	6.266	0.0408
Lake area	−0.1786	0.522	5.588	0.0500
Intercept = −1.368				

TABLE 6. Variable selection in stepwise multiple regression of predicted mercury concentration in a hypothetical 10-g crayfish on conductivity ($\log_{10}$), DOC, K.

Variable	Slope	Cumulative R^2	F	P
Conductivity	−0.540	0.543	11.694	0.009
Intercept = −0.2057				

Comparisons among Lakes for each Crayfish Species

Within each species, the rate at which crayfish bioaccumulated Hg with weight (as indicated by the slope) did not differ among lakes. We found, however, significant differences in intercepts.

For *C. bartoni*, Hg values were highest for Lake Vernon and significantly different ($P<0.05$) from those in Bear Lake; both lakes were also significantly different from the rest of the lakes. Hg values in *C. robustus* were significantly higher ($P<0.001$) in Dickie Lake than in Gull Lake. For *O. propinquus*, values

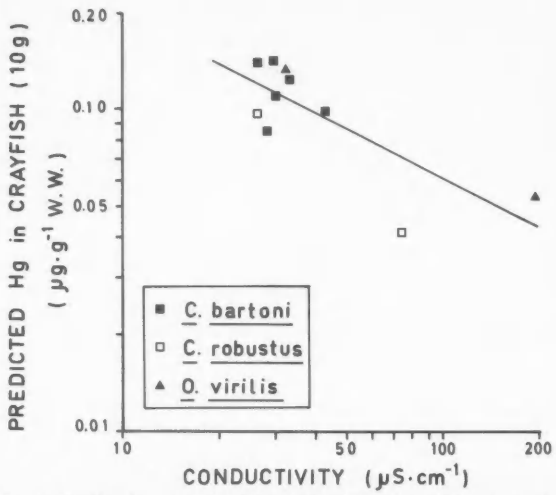

FIG. 2. Predicted mercury in abdominal weight of crayfish at a standard weight of 10 g in relation to lake water conductivity in 10 of our study lakes (Bear, Dickie, Four Mile, Gull, Kimball, Little Hawk, Opeongo, Rebecca, Round, and Waseosa), where:

$$\text{Log Hg}_{\text{cfish}} = -0.504 \text{ Log cond.} - 0.206,\ r=0.771,\ P<0.01.$$

were higher ($P<0.001$) in Waseosa Lake than in Four Mile Lake. For *O. virilis*, the three lakes from which we have data are significantly different ($P<0.001$) from each other: Hg values were highest in Waseosa, intermediate in Rebecca and lowest in Four Mile.

Within each species of crayfish, Hg levels are higher in the less well buffered waters, as it was expected from the relationship established previously between Hg values of pooled species and water chemistry.

Discussion

A wide range of mercury concentrations was observed in abdominal muscle of crayfish for the 13 lakes in this study. From these lakes, remote from known point sources of Hg, total Hg in muscle ranged from 0.02 to 0.64 $\mu g \cdot g^{-1}$ wet weight. These values are considerably lower than the value of 10 $\mu g \cdot g^{-1}$ in crayfish from heavily contaminated Clay Lake (Armstrong and Hamilton 1973), but they fall within the range reported by Rada et al. (1986) in a Hg contaminated system and by Wren et al. (1986) in uncontaminated Muskoka lakes. Concentrations of Hg in benthic invertebrates living in uncontaminated sediments are usually less than 0.1 ppm (Huckabee et al. 1979). The concentrations observed in our study are therefore higher than what should have been expected in ecosystems uncontaminated by point sources of Hg.

Mercury concentrations in abdominal muscle of crayfish were positively correlated with crayfish weight in the five crayfish species (*C. bartoni, C. robustus, O. obscurus, O. propinquus, O. virilis*) which are common in Ontario. It is the first time that such a relationship has been observed in lakes with no direct source of Hg, although such a relationship was found by Vermeer (1972) in *O. virilis* from the Hg polluted Clay Lake. Several authors have reported an absence of relationship between size and Hg in crayfish (Rada et al. 1986; Mathers and Johansen 1985). Perhaps inadequate number of organisms and insufficient range of sizes could account for the failure to detect a Hg–

weight relationship in these studies. The positive relationship that we observed between crayfish Hg and crayfish weight is similar to that described for fish, where it is generally assumed that Hg concentration increases with fish size or age, (Mathers and Johansen 1985; Andersen et al. 1986). Methylmercury, the predominant form of Hg in fish, is slowly metabolized or eliminated from fish and may bioaccumulate in tissues over time because the rate of uptake is more rapid than the clearance (Norstrom et al. 1976). It is likely that such a situation also applies to crayfish, even though the lifespan of crayfish is usually less than 3 yr, i.e. much shorter than for most fish species.

The bioaccumulation patterns of Hg were not quantitatively similar for all species. In *O. propinquus*, the increase in Hg with size was significantly faster than for all other species. Differences in life cycle among species might explain why *O. propinquus* reached higher Hg concentrations at a smaller size than other species. *O. propinquus* is the smallest crayfish species in Ontario (Crocker and Barr 1968). Maturity in *O. propinquus* is reached earlier in time (sometimes in the first year of life) and at a smaller size than in *O. virilis* which reaches maturity in its second year (Crocker and Barr 1968) or in *C. bartoni* and *C. robustus* where maturity is reached in the second or third year (Hamr and Berrill 1985).

In fish Hg studies, lake volume, maximum depth, watershed area/lake volume ratio (in headwater lakes) were related to fish Hg (Wren and MacCrimmon 1983; Suns et al. 1987). In our study, crayfish Hg was mainly related to water chemistry of the lakes. Conductivity alone explained 54% of the variability observed in predicted crayfish Hg. Conductivity was also highly correlated with Ca ($r=0.988$), Mg ($r=0.981$), alkalinity ($r=0.942$), pH ($r=0.866$) and Na ($r=0.818$). This implying that crayfish Hg is related to the buffering capacity of the lakes, and therefore could be affected by acidification. Mercury concentration in abdominal muscle (including exoskeleton) of *O. virilis* in experimentally acidified Lake 233 of the Experimental Lake Area was twice that of the control (France 1987). Similar observations have also been made for fish Hg. For example, lakewater pH was inversely correlated with whole body concentrations of Hg in yearling yellow perch (Suns et al. 1987) and in pumpkinseeds (Wren and MacCrimmon 1983) from lakes in South-Central Ontario. Scheider et al. (1979) observed that fish Hg was higher in low alkalinity (0–15 $mg \cdot L^{-1}$) than in higher alkalinity (>15 $mg \cdot L^{-1}$) lakes. Calcium also plays a role on the uptake efficiency of methylmercury in fish. Rodgers and Beamish (1983) found that the uptake efficiency was more than doubled when fish were placed in softwater as compared with hardwater. Wren and MacCrimmon (1983) showed that calcium was one of the most important variables associated with Hg concentrations in pumpkinseeds. In Suns et al. (1987) study, DOC explained some of the variability found in fish Hg. In our study, no correlation was observed between crayfish Hg and DOC. However, these calculations were for a very small range of DOC and the results might have been different if crayfish data from lakes with higher DOC could have been included in the analysis.

In the two watersheds where both inlet and lake were sampled, inlet crayfish had higher Hg concentration than lake crayfish. Results from a later study on other watersheds showed that crayfish and other invertebrates also displayed the same trend (M. Allard, unpubl. data). We believe this is a novel and interesting observation that deserve more attention since it points out the potential importance of streams in Hg cycling.

Concerning the source of Hg to our lakes and streams, we can only speculate. None of our study lakes is receiving direct discharges of Hg. However, it is possible that Hg is entering in the system through atmospheric deposition. Johnson (1987) showed that Hg enrichment to lake sediment was widespread in Ontario and not only in industrialized areas; the majority of the lakes that he studied had current loadings twice above the background levels. However, new inputs are not the only explanation. As Jernelov (1979) pointed out, there is probably enough Hg in any lake to elevate Hg in the biota, provided that the conditions for methylation are favourable.

Our study showed that smallmouth bass Hg was positively correlated with crayfish Hg, even though the lake (Vernon) with the highest crayfish and fish Hg values had to be removed from the analyses. It is therefore likely that crayfish Hg can contribute to smallmouth bass Hg. In addition, our study also suggested that factors regulating Hg bioaccumulation might be similar for both organisms, even though crayfish have a shorter lifespan, are smaller and have different food habits than fish.

We conclude that crayfish are useful organisms for studying in more detail, the Hg pathways in unpolluted lake with high fish Hg. We suggest specifically that the two stream inhabitant and low pH tolerant *Cambarus* species (Berrill et al. 1985; Hollett et al. 1986) and the streams themselves should be studied in more detail. This will contribute to a better understanding of the high levels in fish Hg in remote lakes. Finally, we suggest that the crayfish *O. propinquus*, could be collected at relatively low cost and become a reliable bioindicator of Hg.

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Impact of Methoxychlor on Selected Nontarget Organisms in a Riffle of the Souris River, Manitoba

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The insecticide methoxychlor was applied at 300 $\mu g \cdot L^{-1}$ for 15 min to a riffle on the Souris River, located about 18 km downstream from Souris, Manitoba. Physical, chemical, and biological variables were measured and aquatic insect community structure was monitored using drift, emergence trap, and artificial substrate samplers. All taxa monitored, irrespective of functional feeding group, drifted catastrophically for 4–24 h immediately following methoxychlor addition. Different species demonstrated varying abilities to recolonize artificial substrates following treatment. Species having a high propensity to drift naturally, recolonized most rapidly. Taxa that required the longest period to recolonize following methoxychlor treatment were generally univoltine, had a low propensity to drift, and a limited ability to disperse as adults. Impact of methoxychlor was influenced by the prevalent life-cycle stage of some species at the time of treatment. *Catostomus commersoni* fry and juvenile *Orconectes virilis* were more sensitive to methoxychlor than previous research on mature individuals has indicated. Invertebrate drift appeared to be more sensitive to pesticide treatment than benthic invertebrates on artificial substrates. Species richness and total numbers of drift were significantly reduced for at least 33 d following treatment, whereas richness and numbers on artificial substrates were significantly lower for only 4 and 8 d, respectively.

On a traité un seuil de la rivière Souris, situé à environ 18 km en aval de la ville de Souris au Manitoba, avec un insecticide, le méthoxychlore, à une dose de 300 $\mu g \cdot L^{-1}$ pendant 15 min. On a mesuré des variables physiques, chimiques et biologiques et on surveillé la structure des populations d'insectes au moyen des techniques suivantes : dérive, piège à émergence et dispositifs d'échantillonnage sur substrat artificiel. Tous les taxons surveillés, sans tenir compte du groupe d'alimentation fonctionnelle, ont dérivé de façon catastrophique pendant 4–24 h, immédiatement après l'addition de métoxychlore. Différentes espèces ont présenté des aptitudes diverses à recoloniser les substrats artificiels à la suite du traitement. La recolonisation a été très rapide chez les espèces ayant une nette tendance naturelle à dériver. Les taxons chez lesquels la recolonisation demande la plus longue période à la suite d'un traitement au métoxychlore étaient généralement des taxons univoltins ayant une faible tendance à dériver naturellement et peu d'aptitude à se disperser à l'état adulte. L'impact du traitement au méthoxychlore a été influencé par le stade dominant du cycle biologique de certaines espèces au moment du traitement. Le frai de *Catastomus commersoni* (Lacépède) et les jeunes *Orconectes virilis* (Hagen) se sont montrés plus sensibles au méthoxychlore que les recherches précédentes sur les individus adultes ne l'avaient indiqué. La dérive des invertébrés a semblé plus sensible aux répercussions du traitement au pesticide, comparativement aux invertébrés benthiques vivant sur des substrats artificiels. On a constaté une diminution significative de la richesse des espèces et du nombre d'organismes ayant dérivé pendant au moins 33 d après le traitement; toutefois cette diminution n'a duré que 4 et 8 jours en ce qui concerne la richesse des espèces et le nombre total d'organismes vivants sur des substrats artificiels, respectivement.

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Blood-sucking black flies are the most serious insect pests affecting both humans and livestock in some regions of western Canada. The most spectacular outbreaks affecting livestock are those of *Simulium arcticum* Malloch from the Saskatchewan and Athabasca rivers. For example, between 1944 and 1948, more than 1300 cattle were killed by *S. arcticum* in Saskatchewan (Fredeen 1977). Black flies landing and crawling about the head, face, and other parts of the body may be unbearable for people engaged in outdoor activities.

In the past, chemicals have been the only significant means by which black flies have been controlled. The earliest toxic chemical used extensively for control was DDT because of its low cost, ease of application, supposed greater selectivity to black fly larvae than to other members of the stream fauna, and its outstanding transport downstream. However, with the discovery of significant effects on nontarget organisms, long-term stability in the environment and biomagnification in the food chain, DDT was banned in 1969 for general use in Canada.

Methoxychlor (2,2-bis-(p-methoxyphenyl)-1,1,1-trichloroethane) was among the first chemicals to be tested in the field

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as a possible replacement for DDT. Over the years, methoxychlor has been the most extensively used chemical in Canada for the control of black files, and it is presently registered for the control of *S. arcticum* and *S. luggeri* Nicholson and Mickel in Saskatchewan and Alberta at a rate of 300 $\mu g \cdot L^{-1}$ for 7.5–15 min. Methoxychlor has also been used to control black flies in northeastern North America (Jamnback 1969; Burdick et al. 1974), and in the Humboldt River in northern Nevada (French et al. 1986).

The numerous conflicting Canadian studies regarding the effects of methoxychlor treatments on nontarget macroinvertebrates (Fredeen 1974, 1975, 1983; Wallace and Hynes 1975; Flannagan et al. 1979, 1980; Depner et al. 1980; Haufe et al. 1980) are usually difficult to interpret because of experimental design (e.g. lack of suitable control stations, inconsistency among habitats sampled, little or no collection of pretreatment data, insufficient replication, improper statistical analyses, identification of invertebrates to generic level or higher; National Research Council of Canada 1983). The objectives of the present study were: (1) to determine what taxa were most adversely affected by methoxychlor addition (300 $\mu g \cdot L^{-1}$ per 15 min) to a riffle of the Souris River; (2) to determine the recovery time for populations and the community of nontarget invertebrates in the riffle; and (3) to determine the relative importance of invertebrate drift from untreated areas upstream in recolonizing the treated riffle.

Methods

Study Sites

The Souris River enters Manitoba from the United States 6.58 km southwest of Lyleton, Manitoba (101°15′W, 49°00′N). It is characterized by a fairly slow current, a high concentration of suspended solids, and little emergent vegetation. Temperatures rise dramatically during the summer, often exceeding 26°C during mid-July. Depth is quite variable (30–400 cm; $\bar{x}$ = 80–100 cm), depending on location and time of year. Dams at Melita, Hartney, Souris, and Wawanesa, Manitoba regulate water flow, except in spring when severe flooding can occur. Discharge varies greatly at different localities during the course of the year (e.g. at Souris, Manitoba in 1976: 275 $m^3 \cdot s^{-1}$ in May; 0.50 $m^3 \cdot s^{-1}$ in October) and from year to year (Westwood and Brust 1981).

The "control" and "treatment" riffle sites selected were located about 18 km downstream from the town of Souris (Fig. 1). Both sites were shallow (mean depth 50 cm) and their substrates consisted of cobble-sized stones and large boulders. The control site was 34–43 m wide × 65 m long, whereas the treatment site, located ≃900 m downstream, was 32–45 m wide × 140 m long. Preliminary sampling indicated a close similarity in the species of aquatic invertebrates inhabiting both sites.

Methoxychlor Addition

An emulsifiable concentrate formulation of methoxychlor (240 $g \cdot L^{-1}$ active ingredient) was applied to the upstream end of the treatment riffle (Fig. 2) on 15 July 1982 at 1200 h. Four litres of methoxychlor (amount calculated to give a theoretical dosage of 300 $\mu g \cdot L^{-1}$ for 15 min, based on river discharge) were thoroughly mixed with 92 L of river water that had been filtered through a fine mesh screen into a 200-L drum. The chemical mixture was pumped through a 20-m length of garden hose that was divided into two additional 10-m long sections. Each 10-m portion was submerged and moved back and forth across half the width of the river just upstream of the treatment riffle to obtain even application of the chemical. The method simulated point-source application in a control program.

Measurements of Water Chemistry and Discharge

Water samples for chemical analysis were collected on 8, 15, 22, 29 July, 17 August, and 16 September 1982. Analysis

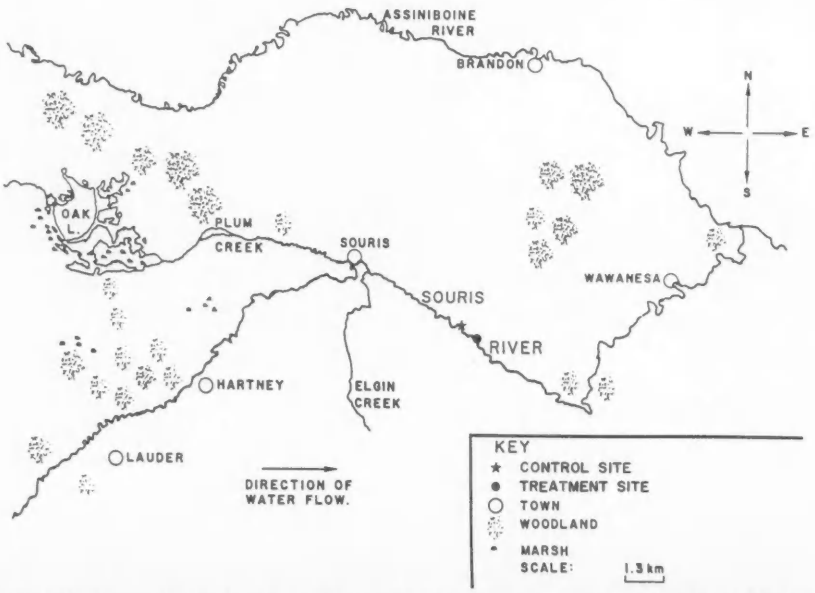

FIG. 1. Study area showing locations of the control and treatment sites on the Souris River, Manitoba.

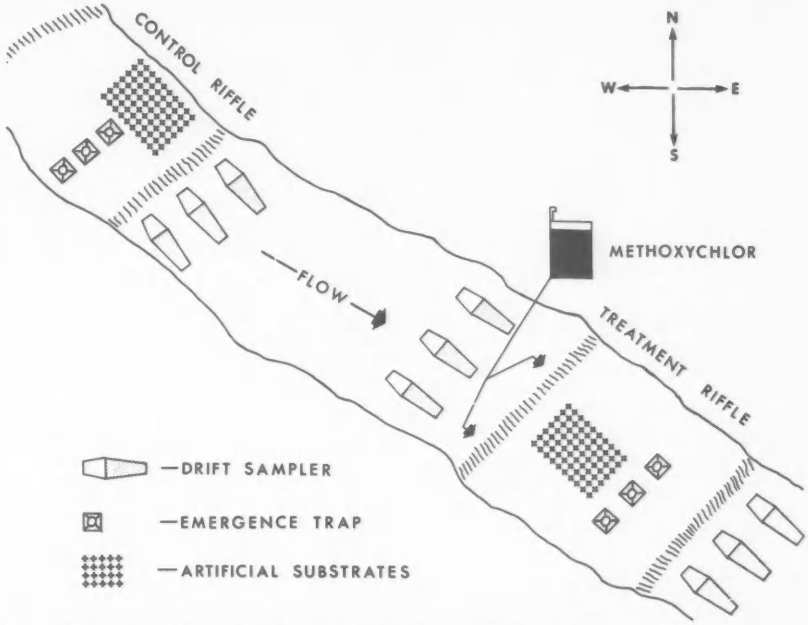

FIG. 2. Arrangement of sampling devices used at the control and treatment sites. Distance from the upstream end of the control riffle to the downstream end of the treatment riffle is ≃900 m.

included pH, total suspended solids (TSS), particulate carbon (PC) and particulate nitrogen (PN). Approximately 900 mL of water were collected in glass jars from the centre of control and treatment sites on each sampling date. Immediately after collection, 1 mL of saturated $HgCl_2$ solution was added to each jar to prevent microbial degradation. The jars were then placed in an ice cooler for transportation to the laboratory, and were stored at 5°C until analyzed. Analyses were performed by the Analytical Chemistry Unit, Water Chemistry Laboratory at the Freshwater Institute, Winnipeg (Stainton et al. 1977). In addition, water temperatures (degrees celsius) were recorded at midday at both sites throughout the study.

Daily discharge measurements (cubic metres per second) for 1982 and 1983 were obtained for the Souris River at Souris, Manitoba, from Manitoba Department of Mines, Resources, and Environmental Management (1982, 1983). Discharge was measured at the site of methoxychlor addition on 14 July 1982 in order to calculate the amount of chemical required to achieve the desired dosage.

Analysis of Methoxychlor Residues in River Water

Water samples for analysis of methoxychlor residues were collected in 1000-mL amber glass jars. Three 900-mL water samples were taken at both the control and treatment sites at each sample period from a transect across each riffle, one from the centre, and one from each side. CH_2Cl_2 (50 mL) was added immediately to each sample jar to ensure complete extraction of methoxychlor from the water sample. The jar was shaken repeatedly and then placed on a magnetic stirrer for 5 min to allow complete mixing of the solvent with the water. Samples were placed in an ice cooler for transportation to the laboratory, and were stored at 5°C until analyzed.

The control and treatment sites were sampled at 24 h before treatment and 10 min, 1, 3, 6, 12, 24, and 48 h after treatment. Three additional samples were taken at each of the 10-min and 1-h posttreatment sampling periods to which sodium azide was added to suppress microbial degradation. Since samples were not analyzed immediately, this provided a check to determine if microbial degradation exerted a significant effect on the concentration of methoxychlor in the samples.

In the laboratory, extraction, clean up, and injection of samples into the gas chromatograph (Tracor Model 565) for residue analysis essentially followed procedures described by Muir and Yarechewski (1984). The minimum detection limit was 0.01 $\mu g \cdot L^{-1}$.

Sampling of Fauna

Three biological variables were monitored: drift, benthos, and emergence. Drift and benthos provided information on recolonization and recovery after methoxychlor treatment. Emergence allowed confirmation of species-level identifications of immatures, and provided the life cycle information necessary to interpret methoxychlor effects on the fauna.

The taxa of interest to this study included all species of Ephemeroptera, Plecoptera, and Trichoptera, the amphipod *Hyalella azteca* (Saussure), the crayfish *Orconectes virilis* (Hagen), and white sucker fry (*Catostomus commersoni* Lacepede). Chironomidae (Diptera) were omitted because of limitations in taxonomy, time, and manpower necessary for species-level identification. All *Baetis* immatures were designated "*Baetis* spp." because most specimens were early instars or had been damaged, and thus could not be identified to species.

Drift

Modified Burton–Flannagan bomb samplers (Burton and Flannagan 1976; Flannagan et al. 1979) with 500-μm Nitex nets were used to collect drift. Three sets of three drift samplers

were positioned in the river (Fig. 2). The "control" set was placed immediately downstream of the control site and measured drift leaving this riffle. The "treatment-inlet" set was placed just upstream of the methoxychlor addition. It sampled drift entering the treatment riffle and provided a measure of recolonization potential. The "treatment-outlet" set was placed immediately downstream of the treatment site, and measured drift leaving the treatment riffle. The three drift samplers at each site were positioned at mid-depth in the water column, evenly spaced across the river.

Drift was sampled prior to (7 and 14 July 1982), during (15 July 1982), and after (21, 29 July and 17 August 1982; 3 August 1983) treatment. On each sampling date, drift samples were collected at 4-h intervals beginning at 0800 h and continuing for 24 h. Additional samples were taken at 1300 and 1400 h on the treatment date at the treatment-outlet site in order to prevent clogging of nets by large numbers of invertebrates induced to drift by the methoxychlor treatment (1200 h). Samples were immediately preserved in 10% formalin. Rose Bengal stain was added to each sample to aid sorting efficiency.

Water velocities were measured directly upstream of the opening of each drift sampler, using a Gurley Model 622 current meter, at the beginning and end of each 24-h sampling period, and mean water velocities were calculated for the sampling period. Drift rates (No./4-h period) were standardized to drift densities (No./100 m^3), using mean water velocity, to allow comparisons between samplers and sites (Elliott 1970). Total drift density for individual taxa for each 24-h sample period was obtained by summing drift densities for the six intervals on each sampling date. Times of sunrise and sunset were also recorded for each drift sampling date.

Drift samples were quantitatively subsampled in the laboratory using the technique of Sebastien et al. (1988). However, subsampling of two invertebrate species (*Acroneuria lycorias* (Newman) and *Orconectes virilis*), and one vertebrate (*Catostomus commersoni*), was not necessary due to their low numbers and large sizes.

Benthos

Coarse substrate in the Souris River experimental sites prohibited effective quantitative sampling of the benthos, so artificial substrates (concrete paving bricks (Trieste design), surface area ≈840 cm^2, made by Genstar Materials Ltd., Manitoba Region) were used. A 15 × 10 grid of substrates was placed in the areas of greatest flow in both the control and treatment sites on 8 and 9 June 1982 (Fig. 2), which allowed 4 wk for invertebrate colonization prior to the first sampling date. Ten bricks were removed, downstream-most row first, from each of the three sites on each sampling date. A 500-μm Nitex dip net was held immediately downstream of each brick, the brick was rapidly lifted and placed in a 12-L plastic pail. Any invertebrates found in the net were added to the pail. The samples were preserved in 75% ethyl alcohol and returned to the laboratory for sorting and identification.

Artificial substrates were sampled prior to (7, 12, and 14 July 1982), and up to a year following treatment (16, 19, 23, 29 July, 16 August, and 17 September 1982; 18 July and 3 August 1983) to assess recolonization and recovery of the benthos (National Research Council of Canada 1983). Artificial substrates sampled in 1983 were installed on 21 June 1983.

Insect emergence

Three pyramidal emergence traps (Westwood and Brust 1981; Sebastien 1986) were placed in each of the control and treatment riffles (Fig. 2), and were emptied after a 48-h collecting period at various dates before (8 and 14 July 1982) and up to 1 mo following methoxychlor addition (17, 19, 22, 28 July, and 18 August 1982). Adult insects were aspirated from the collection jar and the inside of the trap after slowly raising the trap above the water. Specimens were preserved in 75% ethyl alcohol for later identification.

Statistical Analysis

Numbers

The effects of methoxychlor on macroinvertebrate drift densities, numbers on artificial substrates, and numbers emerging, for individual taxa and totals of taxa, were compared between control and treatment sites using two-way analysis of variance (ANOVA) (Snedecor and Cochran 1981). The mean square for the time and site (control, treatment) interaction was used as an error term to test for treatment effects (Green 1979). A $\ln(x+1)$ transformation, as indicated by Taylor's power law (Taylor 1961), was used to remove the dependence of the variance on the mean observed for individual taxa in drift, artificial substrate, and emergence samples.

The two-way ANOVA's used a repeated measures design with two treatments (control, treatment) and no replication of treatments. The time and site interaction was further partitioned among dates using a priori multiple comparisons to compare the difference between the overall control and treatment site means prior to treatment, with the difference between the control and treatment site means on each posttreatment sampling date (Snedecor and Cochran 1981). The H_0 for these comparisons was: methoxychlor treatment does not affect observed pretreatment differences between control and treatment sites for drift density, numbers on artificial substrates or numbers emerging. The above analysis was used to determine the impact of methoxychlor on invertebrates at the treatment site, in comparison to the control site, by taking into account the difference between the control and treatment sites prior to treatment. An example ANOVA table using drift density data for *Caenis tardata* McDunnough is presented in Appendix A.

Like most ecosystem-level manipulations, this study involved "pseudoreplication" because there was no true replication of treatments (Hurlbert 1984). Therefore, in a strict sense, statistical differences between control and treatment sites cannot be attributed to treatment effects. Significant differences actually only demonstrate that species did not show the same (parallel) trends at control and treatment sites for the variable being measured, although departure from these parallel trends coincident with methoxychlor addition strongly implies an effect due to the pesticide.

Species richness

Numbers of species were counted for each replicate sample on each date for both control and treatment sites, so that means and standard errors could be calculated. Species richness in the drift was expressed as mean number of species/24-h period; on artificial substrates it was expressed as mean number of species/840 cm^2 of surface area. Taylor's power law indicated that the variance of species counts was independent of the mean and no transformation was necessary for statistical analysis. The same analyses as described above were used to test for differences in numbers of species in the drift and on artificial substrates between the control and treatment sites.

TABLE 1. Methoxychlor residues (micrograms per litre) in water samples taken from the north (N), middle (M), and south (S) sides of the treatment site before and after methoxychlor addition to the Souris River, Manitoba. Concentrations at the control site were always below minimum detection limits (0.01 $\mu g \cdot L^{-1}$; N/D). * Indicates samples to which sodium azide was added immediately following collection. N/A = not available.

	Treatment site		
Sampling period	N	M	S
Pretreatment (24 h):	N/D	N/D	N/D
Posttreatment:			
10 min	284.44	358.97	223.85
10 min*	282.20	306.88	229.74
1 h	2.08	N/A	2.21
1 h*	2.86	3.08	1.11
3 h	0.26	0.41	0.24
6 h	0.05	0.12	0.03
12 h	0.02	0.06	0.02
24 h	N/D	N/D	N/D
48 h	N/D	N/D	N/D

Results

Water Chemistry and Discharge

The control and treatment sites were similar based on temperature, pH, PC, PN, and TSS. Mid-day water temperatures at control and treatment sites reached a maximum of 25.0°C on 15 July 1982, and declined steadily to 12.5°C on 16 September 1982. pH ranged from 7.6–8.4 over the sampling period but no pattern was obvious between sites or dates. Similarly, there were variations in PC (890–1880 $\mu g \cdot L^{-1}$ at control; 1150–2220 $\mu g \cdot L^{-1}$ at treatment), PN (134–289 $\mu g \cdot L^{-1}$ at control; 121–290 $\mu g \cdot L^{-1}$ at treatment), TSS (9–15 $mg \cdot L^{-1}$ at control; 10–14 $mg \cdot L^{-1}$ at treatment) over the sampling period. Only one sample was collected from each site on each sampling date for chemical analyses so no estimates of variation were possible.

Peak discharges of 78–90 $m^3 \cdot s^{-1}$ occurred in spring and declined to levels below 10 $m^3 \cdot s^{-1}$ by 1 July in 1982 and 1983 (Manitoba Department of Mines, Resources, and Environmental Management 1982, 1983). Discharge at the study site on the day of methoxychlor treatment was 3.3 $m^3 \cdot s^{-1}$.

Methoxychlor Residues in River Water

No detectable methoxychlor residues were observed at the control site on any sampling period before or after methoxychlor addition. At the treatment site, water samples taken 10 min after beginning the addition contained methoxychlor concentrations very close to the desired concentration of 300 $\mu g \cdot L^{-1}$ (Table 1). Trace levels were detected up to 12 h after treatment, but no residues were detected by 24 h. A dense growth of filamentous algae may have retarded passage of methoxychlor through the riffle, which could account for the relatively long period that methoxychlor was detected in the water column. Methoxychlor residues in water samples to which sodium azide was added were similar to residues observed in untreated samples collected simultaneously, indicating that microbial degradation did not significantly alter the methoxychlor concentrations prior to analysis.

Drift

Total drift of taxa

Catastrophic drift of aquatic invertebrates occurred immediately following methoxychlor treatment (Table 2), similar to responses shown in other lotic ecosystems (Burdick et al. 1968; Wallace et al. 1973; Wallace and Hynes 1975; Flannagan et al. 1979). Drift densities at the treatment-outlet site were significantly greater ($p<0.0001$) than at the control site for all invertebrate taxa during the 24-h period after treatment. Moreover, all functional feeding groups were simultaneously affected (predators: *A. lycorias* and *Polycentropus cinereus* (Hagen); scrapers: *Baetis* spp., *C. tardata*, *Leucrocuta maculipennis* (Walsh), *Hydroptila ajax* Ross, *Psychomyia flavida* Hagen, and *Stenacron interpunctatum* (Say); filter feeders: *Cheumatopsyche campyla* (Ross), *Hydropsyche alternans* (Walker), and *Isonychia sicca* Walsh; and collector-gatherers: *Ephoron album* (Say)). Total drift density, and drift densities of most species, were significantly depressed ($p<0.05$) at the treatment-outlet site relative to the control site for all subsequent sampling dates in 1982. Absence in the drift, extremely low drift densities, or high variability prevented the detection of any statistically significant differences ($p<0.05$) between the sites on other than the treatment date for *P. flavida*, *P. cinereus*, *A. lycorias*, and *O. virilis*. Drift densities of only *I. sicca* and *E. album* remained significantly ($p<0.05$) reduced at the treatment-outlet site relative to the control on 3 August 1983.

Species richness

A significantly higher ($p<0.05$) number of species was observed in the drift at the treatment-outlet site relative to the control site on the treatment date (Table 2). The number of species drifting was significantly ($p<0.05$) reduced at the treatment-outlet site compared with the control site for all sampling dates after treatment in 1982 but not by 3 August 1983.

Drift patterns of individual taxa

The response of individual taxa following methoxychlor treatment was categorized according to drift densities at the treatment-inlet site and the length of time required to recover on artificial substrates (see below). Five categories were established: (1) species naturally drifting in high numbers and showing no reduction on artificial substrates (e.g. *C. tardata*); (2) species naturally drifting in moderate to high numbers and recovering rapidly (<8 d) on artificial substrates (e.g. *Baetis* spp. and *L. maculipennis*); (3) species naturally drifting in low to moderate numbers, emerging during the treatment period and showing either no effect, or recovering moderately quickly (<64 d) on artificial substrates (e.g. *H. ajax* and *C. campyla*); (4) species naturally drifting in very low numbers, and recovering slowly on artificial substrates (>64 d, and possibly up to 1 yr following treatment) (e.g. *P. flavida* and *H. alternans*); and (5) species usually occurring in low numbers in the drift, and either absent or occurring in very low numbers on the artificial substrates (e.g. *E. album*, *I. sicca*, *S. interpunctatum*, *P. cinereus*, *A. lycorias*, *H. azteca*, and *O. virilis*). Treatment effects on group (5) species were difficult or impossible to assess, so most drift data presented below concern representative species from each of the first four categories. Complete drift data can be found in Sebastien (1986).

Group 1 species — The mayfly *C. tardata* drifted in high numbers under natural conditions at all sites, and demonstrated a diel periodicity with peak densities occurring during periods of darkness (Fig. 3). The catastrophic drift observed exceeded

TABLE 2. Geometric means and SE factors[a] for 24-h drift densities (No.·100 m^{-3}) of invertebrates and sucker fry at the control (C) and treatment-outlet (T) sites in the Souris River before and after treatment with methoxychlor. Significant differences are based on a priori multiple comparisons (see methods for explanation).

		Pretreatment 1982	Treatment 1982	Posttreatment 1982			1983
		7 and 14 July[b]	15 July	21 July	29 July	17 August	3 August
Baetis spp.[c]	C	107.4⁄1.2	175.0⁄1.4**	199.7⁄1.1*	395.2⁄1.4*	650.6⁄1.4*	225.7⁄1.2
	T	259.5⁄1.1	12755.4⁄1.4	16.5⁄1.3	123.8⁄1.5	189.5⁄1.4	689.9⁄1.2
Caenis tardata	C	144.4⁄1.1	303.8⁄1.2**	135.6⁄1.1*	222.5⁄1.6*	972.8⁄1.2*	225.5⁄1.3
	T	648.7⁄1.1	18882.4⁄1.3	22.6⁄1.4	75.7⁄1.7	577.6⁄1.2	373.3⁄1.2
Leucrocuta maculipennis	C	52.7⁄1.2	78.6⁄1.4**	59.6⁄1.3*	114.9⁄1.5*	77.7⁄1.2*	43.9⁄1.1
	T	94.1⁄1.1	12688.0⁄1.2	3.9⁄2.0	27.6⁄1.8	31.5⁄1.3	131.4⁄1.4
Stenacron interpunctatum	C	4.8⁄1.7	16.2⁄1.5**	2.8⁄1.3*	3.6⁄1.4*	7.6⁄1.4*	42.8⁄1.3
	T	25.3⁄1.1	3886.1⁄1.4	0.0±0.0	1.8⁄1.8	4.0⁄1.1	142.8⁄1.4
Isonychia sicca	C	22.4⁄1.4	52.6⁄1.5**	26.9⁄1.1*	19.8⁄1.4*	9.3⁄1.4*	10.7⁄1.3*
	T	43.8⁄1.2	11067.4⁄1.3	1.6⁄1.6	0.0±0.0	0.0±0.0	2.2⁄1.5
Ephoron album	C	6.3⁄1.4	2.4⁄2.4**	0.0±0.0*	1.9⁄1.5*	2.4⁄1.3*	1.5⁄1.5*
	T	39.7⁄1.3	2344.8⁄1.5	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Hydroptila ajax	C	145.8⁄1.3	127.2⁄1.5**	19.1⁄1.7*	141.8⁄2.2	37.4⁄1.2*	55.5⁄1.4
	T	326.9⁄1.3	2563.6⁄1.6	1.6⁄1.6	107.7⁄1.7	7.9⁄1.0	102.9⁄1.3
Cheumatopsyche campyla	C	5.9⁄1.0	25.8⁄1.1**	13.3⁄1.3*	5.5⁄2.4	87.3⁄1.3	18.5⁄1.7
	T	9.8⁄1.4	20549.0⁄1.4	0.0±0.0	4.4⁄2.1	29.7⁄1.2	54.4⁄1.3
Hydropsyche alternans	C	2.9⁄1.4	3.1⁄1.8**	2.5⁄1.2*	2.1⁄1.6*	19.5⁄1.1*	21.9⁄1.3
	T	13.1⁄1.1	3178.6⁄1.4	1.5⁄1.5	0.0±0.0	8.0⁄1.4	58.3⁄1.3
Pyschomyia flavida	C	1.2⁄1.1	1.6⁄1.6**	0.0±0.0	5.5⁄2.1	3.3⁄1.8	1.6⁄1.6
	T	1.9⁄1.5	12103.8⁄1.3	1.8⁄1.8	1.6⁄1.6	0.0±0.0	6.6⁄1.5
Polycentropus cinereus	C	2.6⁄1.7	6.1⁄1.5**	2.6⁄1.6	6.7⁄1.5	0.0±0.0	8.3⁄1.6
	T	0.0±0.0	304.8⁄1.7	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Acroneuria lycorias	C	1.1⁄1.1	0.0±0.0**	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
	T	0.0±0.0	10.4⁄1.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Hyalella azteca	C	92.7⁄1.3	92.7⁄1.1**	57.0⁄1.1*	50.0⁄1.4*	129.2⁄1.3*	19.9⁄1.2
	T	474.0⁄1.2	7208.4⁄1.3	5.7⁄1.6	16.7⁄1.2	65.5⁄1.2	41.4⁄1.2
Orconectes virilis	C	0.0±0.0	1.5⁄1.5**	1.4⁄1.4	0.0±0.0	0.0±0.0	0.0±0.0
	T	0.0±0.0	37.2⁄1.3	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Catostomus commersoni	C	10.8⁄1.6	9.9⁄1.7	0.0±0.0	5.2⁄1.9	7.1⁄1.8*	3.4⁄1.6
	T	9.0⁄1.5	4.7⁄1.2	0.0±0.0	1.1⁄1.1	0.0±0.0	4.7⁄2.4
Total of taxa	C	651.3⁄1.2	951.2⁄1.1**	521.0⁄1.1*	1015.0⁄1.6*	2032.0⁄1.3*	713.3⁄1.0
	T	2092.3⁄1.1	108190.0⁄1.3	51.5⁄1.4	365.7⁄1.6	929.7⁄1.2	1609.1⁄1.2
Species richness[d]	C	11.7±0.4	11.7±1.2*	10.0±0.0*	12.4±0.7*	11.7±0.4*	11.7±0.4
	T	11.2±0.3	15.0±0.0	5.0±0.0	6.7±0.4	8.0±0.0	10.7±0.4

[a]Since the transformation used was $Y = \ln(x+1)$, a value of 1 must be subtracted from the table values to return completely to the original scale. For example, the values in the original scale corresponding to 5.0⁄2.0 are 5 − 1, (5 ÷ 2) − 1 and (5 × 2) − 1, or a geometric mean of 4 and SE of 1.5 to 9.0. (If all observations are zero for any cell in the table, the table values should be 1⁄1 according to the above rule. But to avoid confusion, they were set to 0±0).

[b]Seven and 14 July combined to give overall pretreatment geometric mean and SE calculated from means of the three replicates over the two dates.

[c]Includes *Baetis pygmaeus* (Hagen), *B. flavistriga* McDunnough, *B. brunneicolor* McDunnough, *B. propinquus* (Walsh), *B. pallidulus* McDunnough, and *B. intercalaris* McDunnough.

[d]Since no transformation was used, table values are arithmetic mean (±1SE) number of species in the drift.

*Means are significantly different at $p<0.05$.

**Means are significantly different at $p<0.0001$.

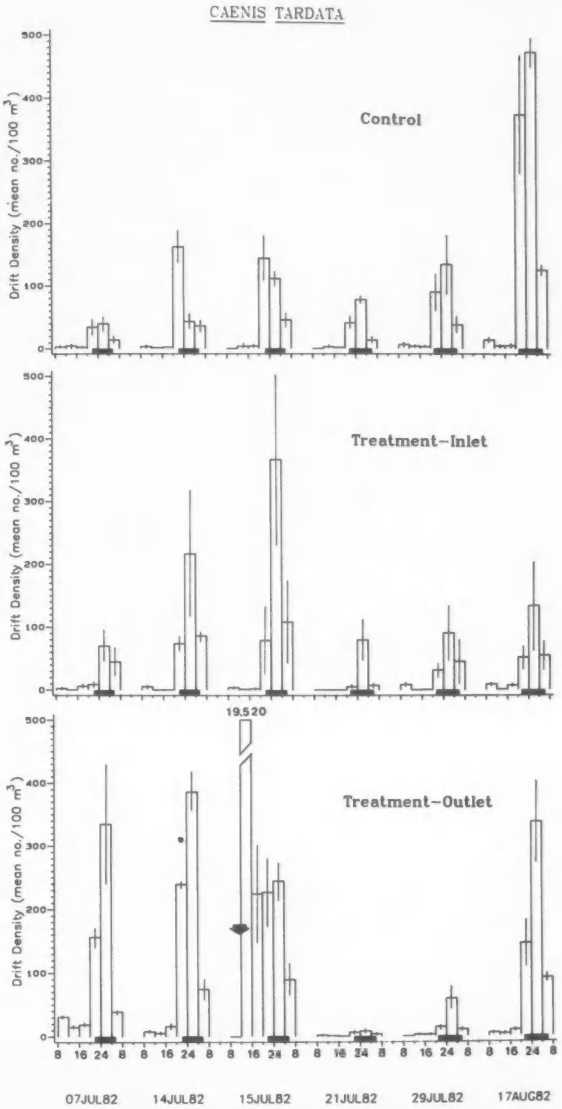

FIG. 3. Mean (±1SE) drift density of *Caenis tardata* larvae at the three sampling sites in 1982. Dark bars = night. Numbers on *x* axis represent 24-h time. Arrow indicates methoxychlor addition.

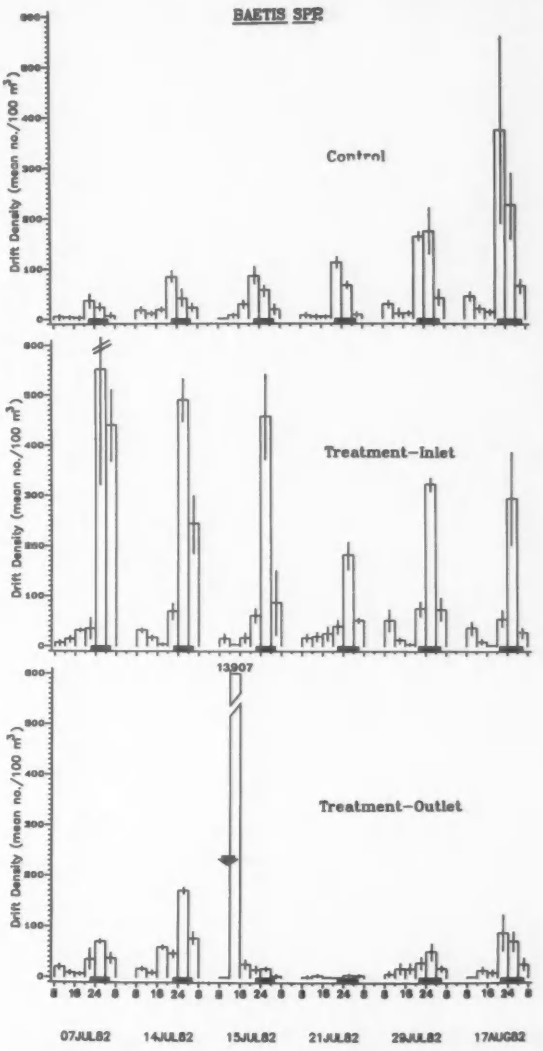

FIG. 4. Mean (±1SE) drift density of *Baetis* spp. larvae at the three sampling sites in 1982. Dark bars = night. Numbers on *x* axis represent 24-h time. Arrow indicates methoxychlor addition.

control drift densities for ‹8 h and was significantly greater ($p<0.0001$) than at the control site for the 24-h period of 15 July 1982 (Table 2). Drift density increased ‹3900 times relative to the control site in the 4 h following treatment. Total 24-h drift densities were significantly lower ($p<0.05$) at the treatment-outlet site compared with the control for all the posttreatment sampling dates in 1982 (Table 2). The sites were not significantly different ($p>0.05$) for 24-h drift densities on 3 August 1983.

Group 2 species — Baetis spp. mayflies drifted naturally in high numbers (especially at the treatment-inlet site), and showed a diel periodicity with peaks corresponding to periods of darkness (Fig. 4). The catastrophic drift peak observed immediately following methoxychlor addition lasted for ‹4 h. Drift was significantly greater ($p<0.0001$) than at the control site for the 24-h period of 15 July 1982 (Table 2). The number of *Baetis* spp. drifting during the 4 h following treatment increased 1900-fold relative to the control site. Total 24-h drift densities were significantly lower ($p<0.05$) at the treatment-outlet site compared with the control site for all the posttreatment sampling dates in 1982. No significant differences ($p>0.05$) were observed for 24-h drift densities between the two sites on 3 August 1983.

Group 3 species — The caddisfly *H. ajax* drifted in relatively high densities at the control and treatment-outlet sites but in very low densities at the treatment-inlet site, and showed no

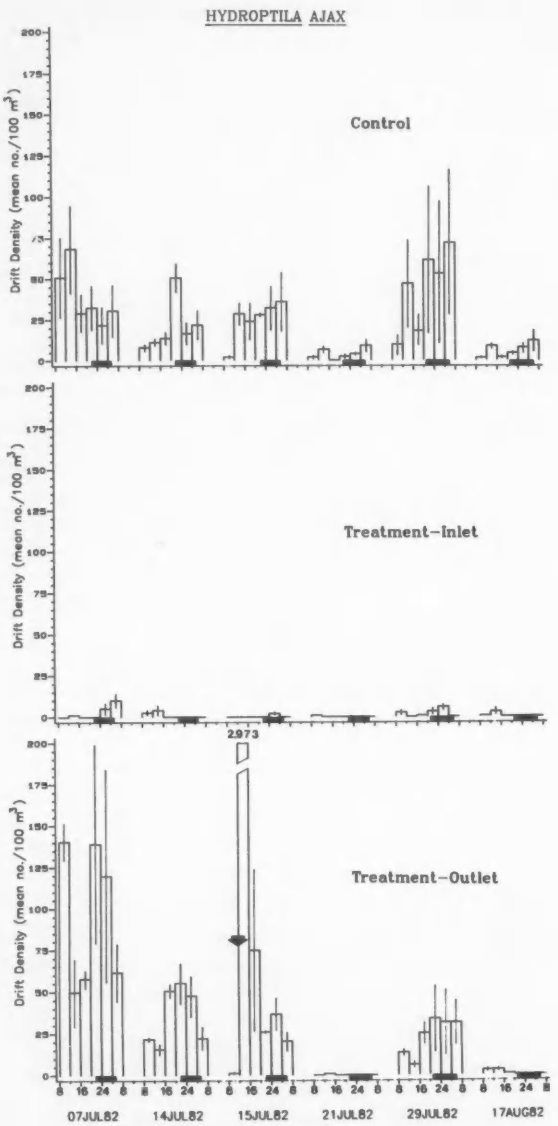

FIG. 5. Mean (± 1SE) drift density of *Hydroptila ajax* larvae at the three sampling sites in 1982. Dark bars = night. Numbers on *x* axis represent 24-h time. Arrow indicates methoxychlor addition.

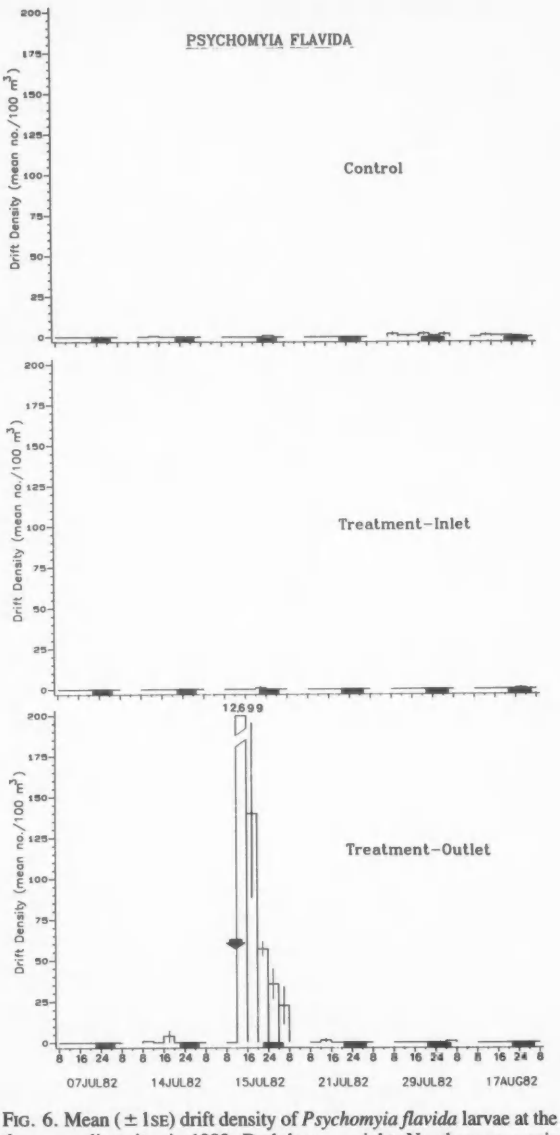

FIG. 6. Mean (± 1SE) drift density of *Psychomyia flavida* larvae at the three sampling sites in 1982. Dark bars = night. Numbers on *x* axis represent 24-h time. Arrow indicates methoxychlor addition.

diel drift periodicity (Fig. 5). The catastrophic drift observed exceeded drift densities at the control site for ‹8 h and was significantly greater ($p<0.0001$) than at the control site for the 24-h period of 15 July 1982 (Table 2). Drift densities increased 104 times relative to the control site in the 4 h following treatment. Drift density (24-h) was significantly lower ($p<0.05$) at the treatment-outlet site compared with the control on 21 July 1982. An increase in drift density occurred at both sites on 29 July 1982 that resulted in no significant difference ($p>0.05$) for 24-h drift density between the two sites. Drift density (24-h) was again significantly lower ($p<0.05$) at the treatment-outlet site relative to the control on 17 August 1982. The sites were not significantly different ($p>0.05$) on 3 August 1983.

Group 4 species — The caddisfly *P. flavida* rarely drifted under natural conditions, but large numbers drifted following methoxychlor treatment (Fig. 6). Drift density at the treatment-outlet site increased 12 700 times that of the control site in the 4 h following methoxychlor addition. Elevated drift densities lasted for ‹24 h following treatment, and they were significantly greater ($p<0.0001$) than at the control site for this period (Table 2). Drift densities (24-h) were not significantly different ($p>0.05$) between the control and treatment-outlet sites on any of the posttreatment sampling dates in 1982, or on 3 August 1983.

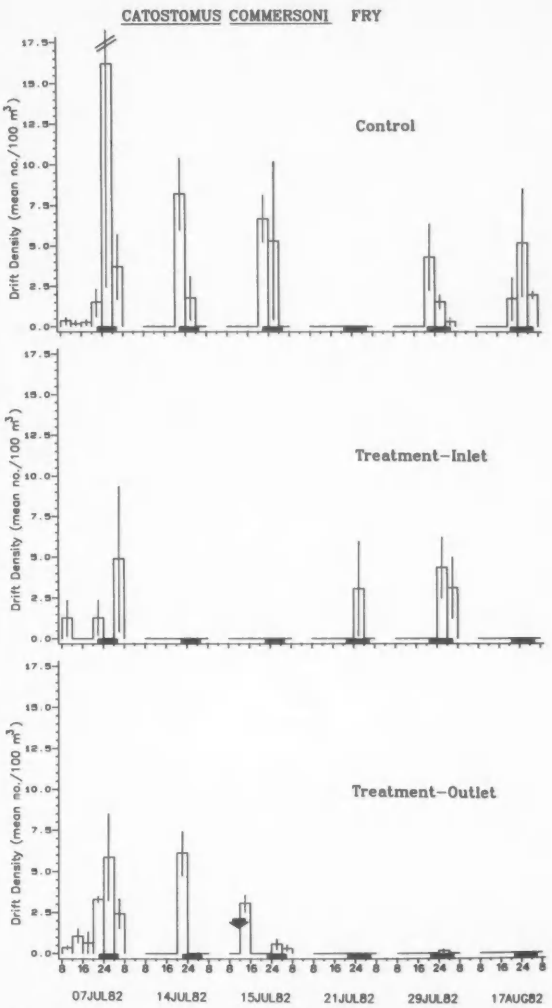

FIG. 7. Mean (±1SE) drift density of *Catostomus commersoni* fry at the three sampling sites in 1982. Dark bars = night. Numbers on *x* axis represent 24-h time. Arrow indicates methoxychlor addition.

Drift of sucker fry

Catostomus commersoni fry drifted naturally, and showed a diel periodicity with maximum numbers occurring during the night (Fig. 7). Drift density (24-h) was only significantly lower ($p<0.05$) at the treatment-outlet site relative to the control on 17 August 1982, but on no other dates in 1982 or 1983 (Table 2). However, a slight increase in drift density of the fish fry occurred at the treatment-outlet site relative to the control that lasted for ‹4 h following methoxychlor treatment. Fry were virtually absent from the drift on posttreatment sampling dates in 1982 at the treatment-outlet site (cf. pretreatment levels at that site and posttreatment levels at both the control and treatment-inlet sites; Fig. 7).

Artificial Substrates

Total numbers

Total numbers (all taxa) on artificial substrates were significantly reduced ($p<0.05$) at the treatment site relative to the control site on all sampling dates following treatment in 1982, except at 14 d (Table 3). However, the significant differences ($p<0.05$) observed between sites on 16 August and 17 September 1982 were due to very large numbers of *H. alternans* (geometric mean numbers = 277.3 and 478.4, respectively) observed on control artificial substrates. The difference between control and treatment sites on these dates was not significant ($p>0.05$) when *H. alternans* was removed from the analysis. Significant differences were not found ($p>0.05$) between sites in 1983 (Table 3).

Species richness

Species richness was significantly reduced ($p<0.05$) at the treatment site relative to the control site for at least 4 d after treatment, but no significant differences ($p>0.05$) occurred between sites for the remaining sampling dates in 1982 and 1983 (Table 3).

Individual taxa

Individual taxa recolonized the artificial substrates at different rates following methoxychlor treatment (Table 3). Recolonization of some species was rapid. For example, numbers of *L. maculipennis* and *Baetis* spp., both Group 2 species, were significantly lower ($p<0.05$) at the treatment site only for day 1 and days 1 and 4, respectively (Table 3). Other taxa remained significantly reduced ($p<0.05$) at the treatment site relative to the control site for the majority of sampling dates, including the last one, in 1982 (e.g. *H. alternans* and *P. flavida*, both Group 4 species). *Cheumatopsyche campyla*, a Group 3 species, apparently had recovered by 17 September 1982 (64 d after treatment). Numbers of some taxa on the artificial substrates appeared to be enhanced following the treatment, e.g. *H. ajax* (Group 3) and *C. tardata* (Group 1). *Ephoron album*, juvenile *O. virilis* and *C. commersoni* fry were not included in Table 3 because they were never collected from artificial substrates, and numbers of *I. sicca, S. interpunctatum, A. lycorias, P. cinereus,* and *H. azteca*, all Group 5 species, were too low to allow meaningful statistical analysis.

Drift–Benthos Relationships

Although numbers of many taxa and total numbers on artificial substrates (exluding *H. alternans*) had recovered at the treatment site by 14 d after treatment (Table 3), drift densities of the majority of taxa and total drift density remained significantly reduced ($p<0.05$) for all sampling dates in 1982 (Table 2). In fact, numbers in the drift may have required until the following summer to reach pretreatment levels (Fig. 8).

Insect Emergence

Adults of *P. flavida, P. cinereus, I. sicca, H. alternans, S. interpunctatum, Baetis propinquus, B. pallidulus, B. intercalaris, B. flavistriga, H. ajax, C. campyla, Hydropsyche sparna* Ross, *H. bifida* Banks, *H. betteni* Ross, and *Nixe inconspicua* (McDunnough) were collected from emergence traps at both sites in 1982, but only *H. ajax* and *C. campyla* occurred in sufficient numbers for analysis.

Peak emergence of *H. ajax* occurred soon after treatment, and numbers emerging were significantly lower ($p<0.05$) at the treatment site relative to the control 4, 7, and 13 d after treatment (Table 4). However, the sites were not significantly different ($p>0.05$) by 18 August 1982, 34 d after treatment (Table 4). Emergence of *C. campyla* was significantly reduced ($p<0.05$) at the treatment site relative to the control on all sampling dates, except 2 and 13 d, following treatment (Table 4).

TABLE 3. Geometric means and SE factors[a] for numbers of invertebrates on artificial substr
methoxychlor. Methoxychlor was added on 15 July 1982. Significant differences are b

		Pretreatment 1982			
		7, 12, and 14 July[b]	16 July	19 July	
Baetis spp.[c]	C	39.0×1.1	21.5×1.2*	25.6×1.3*	1
	T	29.3×1.2	1.1×1.1	1.7×1.3	
Caenis tardata	C	1.9×1.2	1.5×1.2	0.0±0.0	
	T	3.1×1.2	4.4×1.3	3.1×1.4	
Leucrocuta maculipennis	C	5.6×1.2	9.4×1.5*	4.5×1.4	
	T	6.6×1.2	1.4×1.2	1.8×1.3	
Isonychia sicca	C	2.4×1.1	1.6×1.2*	3.7×1.4*	
	T	4.3×1.2	1.4×1.1	1.1×1.1	
Stenacron interpunctatum	C	1.1×1.1	1.2×1.1	1.1×1.1	0
	T	1.1×1.1	0.0±0.0	1.1×1.1	
Acroneuria lycorias	C	1.0×1.0	1.1×1.1	0.0±0.0	
	T	1.0×1.0	0.0±0.0	1.1×1.1	0
Hydroptila ajax	C	32.2×1.3	3.2×1.5*	1.8×1.4	
	T	65.8×1.2	37.8×1.1	3.7×1.4	1
Hydropsyche alternans	C	12.9×1.3	3.9×1.5	12.8×1.4*	
	T	5.3×1.2	1.2×1.1	1.4×1.2	0
Cheumatopsyche campyla	C	6.3×1.2	6.4×1.3	8.6×1.2*	1
	T	8.3×1.1	3.0×1.3	1.1×1.1	
Psychomyia flavida	C	3.8×1.2	74.8×1.3*	105.5×1.3*	1
	T	3.8×1.3	2.5×1.3	1.7×1.2	
Polycentropus cinereus	C	1.2×1.1	1.9×1.2*	1.5×1.2	
	T	1.3×1.1	0.0±0.0	1.2×1.1	
Hyalella azteca	C	2.9×1.2	0.0±0.0	0.0±0.0	
	T	5.0×1.2	1.7×1.2	1.8×1.3	
Total of taxa	C	146.8×1.1	144.5×1.1*	200.1×1.1*	9
	T	177.5×1.1	50.9×1.1	13.7×1.2	4
Species richness[d]	C	7.1±0.2	6.7±0.5*	6.6±0.3*	5
	T	7.5±0.2	5.1±0.3	4.3±0.6	5

[a]See footnote "a", Table 2.
[b]7, 12, and 14 July combined to give overall pretreatment geometric mean and SE cal
the three dates.
[c]See footnote "c", Table 2.
[d]Since no transformation was used, table values are arithmetic mean (±1SE) number
*Means are significantly different at $p<0.05$.

al substrates at the control (C) and treatment (T) sites in the Souris River before and after treatment with
es are based on a priori multiple comparisons (see methods for explanation).

Posttreatment 1982				1983	
23 July	29 July	16 August	17 September	18 July	3 August
18.9±1.3	35.5±1.2	42.1±1.2	5.6±1.3	12.0±1.2	35.4±1.2
9.9±1.6	35.7±1.3	60.6±1.2	5.0±1.3	16.9±1.2	44.9±1.2
1.1±1.1*	1.2±1.2	0.0±0.0	1.4±1.2	1.1±1.1	0.0±0.0
6.9±1.4	1.9±1.3	1.5±1.2	1.8±1.2	2.0±1.2	1.3±1.1
3.0±1.4	5.4±1.5	2.5±1.4	1.4±1.2	1.8±1.2	2.0±1.3
1.6±1.2	2.5±1.4	1.4±1.2	1.3±1.2	4.8±1.4	2.6±1.4
1.2±1.1	1.9±1.2*	1.3±1.1*	0.0±0.0	1.5±1.2	1.6±1.2*
1.2±1.1	1.5±1.2	1.1±1.1	1.1±1.1	1.9±1.2	1.2±1.2
0.0±0.0	1.1±1.1	0.0±0.0	0.0±0.0	0.0±0.0	1.5±1.2
1.3±1.2	1.3±1.2	0.0±0.0	1.1±1.1	1.3±1.2	2.0±1.3
1.1±1.1	1.2±1.1	0.0±0.0	0.0±0.0	0.0±0.0	1.1±1.1
0.0±0.0	1.1±1.1	0.0±0.0	1.1±1.1	1.1±1.1	1.1±1.1
2.2±1.4	31.9±1.5	17.9±1.4	4.4±1.4*	3.7±1.4	159.4±1.1*
13.5±1.7	117.6±1.3	87.0±1.2	2.3±1.4	13.3±1.5	55.6±1.1
6.4±1.6*	7.8±1.6*	277.3±1.3	478.4±1.4*	129.1±1.3	126.8±1.3
0.0±0.0	2.0±1.4	63.9±1.4	58.9±1.5	75.6±1.3	81.4±1.4
10.2±1.6*	17.5±1.3*	50.2±1.2*	188.4±1.2	15.3±1.2	30.7±1.2
1.2±1.1	2.8±1.3	17.6±1.3	110.9±1.2	21.6±1.2	38.6±1.2
18.0±1.6*	5.4±1.2	1.7±1.3	31.8±1.1*	25.5±1.2	4.3±1.3
2.7±1.3	2.4±1.4	2.5±1.4	5.0±1.4	16.7±1.1	8.5±1.2
1.2±1.2	1.4±1.2	0.0±0.0	0.0±0.0	1.1±1.1	1.1±1.1
1.1±1.1	1.7±1.2	0.0±0.0	0.0±0.0	1.1±1.1	1.1±1.1
1.1±1.1	1.9±1.3	1.2±1.2	21.1±1.3*	1.1±1.1	0.0±0.0
3.0±1.3	2.2±1.3	1.1±1.1	7.8±1.5	1.3±1.1	1.1±1.1
94.7±1.2*	140.0±1.2	445.8±1.2*	830.6±1.2*	201.3±1.2	390.4±1.1
44.3±1.5	185.3±1.3	268.9±1.2	221.7±1.3	178.5±1.1	259.5±1.2
5.7±0.3	7.7±0.3	5.3±0.4	6.4±0.3	6.1±0.3	6.5±0.5
5.3±0.6	6.7±0.6	5.4±0.3	6.5±0.4	7.8±0.5	7.1±0.5

d SE calculated from means of the 10 replicates over

number of species on artificial substrates.

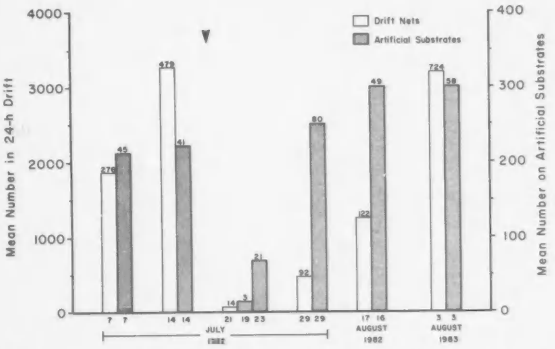

FIG. 8. Mean number of invertebrates drifting over a 24-h period ($n = 3$ for each sample date) from the treatment-outlet site, and on artificial substrates ($n = 10$ for each sample date) at the treatment site. Number above each bar is one standard error of the mean. Drift data for treatment data (15 July 1982) are not included. Arrow indicates methoxychlor addition.

Discussion

Recolonization

Different taxa demonstrated varying abilities to recolonize the artificial substrates following pesticide addition to the Souris River. Some taxa recolonized within days, whereas others required months to recover relative to the control site. This great variation in ability to recolonize probably can be best explained by the major pathways used for recolonization. Williams and Hynes (1976) demonstrated that animals recolonizing an area of denuded stream substrate came from four main sources: downstream drift, upstream migration, upward migration from the hyporheic zone, and egg laying by aerial adults. Drift from upstream areas was the most important source, accounting for ‹40% of the total number that settled in a denuded area. Townsend and Hildrew (1976) determined that drift from areas upstream was responsible for 82% of the recolonization observed in their study. Wallace et al. (1973) observed rapid repopulation of the stream surface substrate, after application of insecticides, and ascribed this to immigration from hyporheic sources. Recolonization by selected taxa in the Souris River is discussed below.

Group 1 species

Although *C. tardata* drifted catastrophically and did not recover until well after methoxychlor treatment (Fig. 3), numbers on artificial substrates were always higher at the treatment site than at the control, significantly so ($p<0.05$) 8 d after treatment (Table 3). The disparity in numbers between treatment and control sites in both types of samples before methoxychlor was added (Table 2 and 3), and the lack of response of *C. tardata* on artificial substrates afterward remain unexplained.

Colonization of artificial substrates can be selective (Rosenberg and Resh 1982), which may explain the overall low numbers of *C. tardata* at both treatment and control sites. The catastrophic drift of *C. tardata* observed must have originated in the natural substrate, but in the absence of samples directly from this habitat we are unable to comment on recolonization by this species.

Group 2 species

Baetis spp. have a high propensity to drift under natural conditions, which probably represents the main method used by nymphs of this genus to recolonize denuded areas of stream. Numbers of *Baetis* spp. on artificial substrates at the treatment site were significantly lower ($p<0.05$) than at the control on days 1 and 4 following methoxychlor addition (Table 3). The rapid recovery on the artificial substrates probably can be explained by the very high densities drifting into the treatment riffle at the treatment-inlet site (Fig. 4). Moreover, five of the six species of *Baetis* collected in this study have bivoltine life cycles; only *B. intercalaris* is univoltine (Clifford 1982). Production of more than one generation per year should enhance recolonization. Therefore, most of the species of *Baetis* probably did not suffer long lasting reductions following the single methoxychlor treatment.

Leucrocuta maculipennis also recovered very rapidly on artificial substrates following methoxychlor treatment (Table 3). This observation also can be explained by high densities drifting into the treatment riffle at the treatment-inlet site (Sebastien 1986, figure 25, appendix A).

Group 3 species

Hydroptila ajax also drifted in high numbers immediately following treatment (Fig. 5). However, the magnitude of its catastrophic drift was less than for most other species of Trichoptera examined (Table 2). Fredeen (1969) suggested that *Hydroptila* and *Brachycentrus* larvae tolerated DDD better than

TABLE 4. Geometric means and standard error factors[a] for numbers of Trichoptera emerging at the control (C) and treatment (T) sites in the Souris River before and after treatment with methoxychlor. Methoxychlor was added on July 15 1982. Significant differences are based on a priori multiple comparisons (see methods for explanation).

		Pretreatment 1982	Posttreatment 1982				
		8 and 14 July[b]	17 July	19 July	22 July	28 July	18 August
Hydroptila ajax	C	8.6×1.1	44.0×1.0	48.0×1.2 *	29.1×1.2 *	26.6×1.4 *	4.2×1.2
	T	12.1×1.2	38.9×1.3	24.9×1.3	5.3×1.1	0.0±0.0	4.6×1.6
Cheumatopsyche campyla	C	0.0±0.0	2.9×1.4	3.2×1.3 *	8.6×1.2 *	6.5×1.8	9.5×1.4 *
	T	1.9×1.4	1.6×1.3	1.3×1.3	4.5×2.2	8.8×1.6	4.7×1.3

[a]See footnote "a", Table 2.

[b]Eight and 14 July combined to give overall pretreatment geometric mean and standard error; calculated from means of the three replicates over the two dates.

*Means are significantly different at $p < 0.05$.

net-spinning larvae because their cases provided protection from the chemical. *Hydroptila ajax* was the only case-bearing caddisfly of the five species examined here.

Hydroptila ajax on artificial substrates did not appear to be affected following methoxychlor addition (Table 3). In fact, numbers were almost always higher at the treatment site than the control site, both before and after treatment, an observation that remains unexplained. An emergence peak roughly coincided with methoxychlor addition (Table 4) indicating that emerging adults were not initially affected by the pesticide. Pupae about to emerge also may be resistant because they are enclosed in silken cases. Later, emergence was significantly depressed ($p<0.05$) at the treatment site relative to the control, perhaps because of an original adverse effect of the treatment on larvae that were about to pupate. *Hydroptila ajax* has a low propensity to drift, so the recolonization that occurred was probably due to egg-laying adults. Flannagan (1977) reported that *H. ajax* was trivoltine in the Roseau River, southeastern Manitoba.

Although emergence of *C. campyla* at the treatment site relative to the control decreased significantly following methoxychlor addition (Table 4), recolonization of the treatment riffle probably occurred mainly by egg-laying adults of this species (cf. Byrtus 1982). Because of its low behavioural drift rate (Sebastien 1986, figure 10) and univoltine life cycle (Flannagan 1977), recolonization at the treatment site probably would have required much longer had emergence not occurred prior to and during methoxychlor treatment.

Group 4 species

Numbers of *P. flavida* were significantly reduced ($p<0.05$) on artificial substrates at the treatment site relative to the control site on all posttreatment sampling dates in 1982 except for 29 July and 16 August (Table 3). However, numbers also were reduced on these dates at the control site, possibly due to an emergence of *P. flavida* that was observed from mid-July to mid-August in the Souris River (R.J. Sebastien, unpubl. data). Egg-laying adults probably were responsible for the subsequent recolonization of *P. flavida*, and increased numbers at the control site on 17 September 1982 likely resulted from a new generation of larvae. Low numbers of *P. flavida* drifting naturally (Fig. 6: see treatment-inlet site) may explain why this species did not recover until the following summer. Also, *P. flavida* is univoltine in the Roseau River (Flannagan 1977), and a univoltine species with a low propensity to drift would be susceptible to long-term reductions by methoxychlor larviciding operations. Because recolonization is most likely by egg-laying adults, a much longer period would be required for this species to recover.

Hydropsyche alternans also required a long time to recolonize the artificial substrates following methoxychlor treatment (Table 3). It too had a low propensity to drift naturally (Sebastien 1986, figure 29, appendix A).

Other invertebrate taxa

It is difficult to comment on recolonization by Group 5 species because of their relative scarcity in samples taken from the Souris River. However, limited data and observations are available for three of the taxa in this group.

Although *E. album* adults were not collected by emergence traps at any time during the study, 538 adults were recovered from the three drift samplers at the control site 14 d after treatment (R.J. Sebastien, unpubl. data). Only 14 adults were collected from the three drift samplers at the treatment-outlet site at the same time. *Ephoron album* nymphs drifted catastrophically at the treatment-outlet site following methoxychlor treatment (Table 2), so the adult population at the treatment site may have been severely reduced by effects of the methoxychlor on immatures. *Ephoron album* drifts in very low numbers under natural conditions (Sebastien 1986, figure 21, appendix A), has a univoltine life cycle (Clifford 1982), and a short-lived adult stage (Giberson and Galloway 1985). Therefore, it should be very susceptible to long-term numerical reduction by repeated methoxychlor treatments.

The predatory stonefly *A. lycorias* also increased in the drift following methoxychlor addition (Table 2), but drift densities were lower than other invertebrate taxa because of its relative rarity at the study sites. *Acroneuria lycorias* occurred on artificial substrates at the treatment site on various posttreatment sampling periods, but numbers were too low to permit any meaningful statistical analysis (Table 3). Although the species is susceptible to methoxychlor (Sebastien and Lockhart 1981; Scherer and McNicol 1986), some individuals were able to survive the methoxychlor injection, as suggested by their presence on artificial substrates at the treatment site only 4 d after treatment.

Orconectes virilis juveniles rarely drifted, but a substantial increase in numbers drifting was observed following methoxychlor treatment (Table 2). *Orconectes virilis* was the least susceptible of several organisms to methoxychlor in the laboratory tests of Merna and Eisele (1973), and Flannagan et al. (1979) found no significant effect on blood calcium and no mortality in caged *O. virilis* after an application of 300 $\mu g \cdot L^{-1} \cdot 15\ min^{-1}$ of methoxychlor to the Athabasca River, Alberta. However, mature specimens were used in these studies, and *O. virilis* juveniles may be far more sensitive to methoxychlor because of higher surface:volume ratios (Sanders and Cope 1968; Wallace and Hynes 1981). Many of the juveniles collected in the catastrophic drift from the Souris River were moribund or dead (R.J. Sebastien, unpubl. data), indicating their susceptibility to methoxychlor treatment.

Downstream effects

Although the experimental design of this study precluded examination of downstream responses to methoxychlor addition in the Souris River, some comment can be made about recovery in areas distant from pesticide application. In general, the theory of island biogeography (MacArthur and Wilson 1963, 1967) can be applied to invertebrate recolonization following black fly larviciding operations in large rivers (see also Gore 1982; Minshall et al. 1983).

Characteristically, methoxychlor is added directly to the water as a point-source application rather than being sprayed over the catchment. Sites closest to pesticide application, although exposed to the highest pesticide concentrations, should have the greatest potential to recolonize rapidly because of their proximity to sources of upstream colonization such as drift and aerial, egg-laying adults. The time required to recolonize should progressively increase with increasing distance downstream from the treatment site. One year after applying methoxychlor to the Athabasca River, invertebrate standing crops at the two furthest downstream sampling sites were still significantly reduced, whereas the upstream sampling sites had completely recolonized (Flannagan et al. 1979). The greatest long-term effect on nontarget invertebrates was observed at the furthest downstream sampling site, 400 km from the treatment site. In rivers, the effect of distance diminishes with time, because

sources of colonization progressively shift downstream. Recolonization also can be influenced by tributaries that act as a source of colonists for treated sections of rivers, although no major tributaries exist in the Souris River downstream from the site of pesticide addition. Currently, no guidelines exist to estimate speed of recovery in lotic systems.

Responses of White Sucker Fry

Mortality of *C. commersoni* fry was not observed at any time during the experiment. However, slightly elevated drift immediately following methoxychlor treatment, during a period when the species does not normally drift (Fig. 7), indicated an avoidance response, and some fry were moribund in the pool downstream of the treatment riffle immediately following treatment. Numbers of alevins and fry of *C. commersoni* increased substantially in the drift 400 km downstream of methoxychlor addition to the Athabasca River (Flannagan et al. 1979), but it was not established that the increase was due to methoxychlor.

Larval fish should be more susceptible to acute poisoning that larger mature fish. Most of the research conducted on the acute toxicity of methoxychlor to native fish species during black fly larviciding operations (e.g. Lockhart et al. 1977; Lockhart 1980) has focused on fish specimens >100 g. However, exposure of 3- to 240-g rainbow trout to methoxychlor resulted in a statistically significant inverse relationship between fish size and methoxychlor uptake (Lockhart 1980). Also, methoxychlor was harmful to juvenile *C. commersoni* in pulse-dosed experiments done in the laboratory (Holdway et al. 1987). Spawning activities of *C. commersoni* could coincide with a methoxychlor larviciding operation, so more research is required to determine the impact of treatment on early life stages of this species.

Community Responses

The recovery of total abundances, species richness, and many individual taxa at the treatment site occurred more slowly in the drift than on the artificial substrates following methoxychlor treatment (Table 2 and 3). Either the artificial substrates provided a less-sensitive measure than drift of impact due to methoxychlor treatment, or invertebrates living in the stream benthos recovered more quickly than those in the drift (Fig. 8).

Dimond (1967) also observed that, in streams with different histories of DDT treatment, drift required one or two seasons after bottom populations had recovered to regain its normal abundance and composition. If stream drift represents a way for invertebrates to seek more preferable habitats and food resources, avoid predation, and regulate population densities (Minshall and Winger 1968; Hildebrand 1974; Walton et al. 1977; Bohle 1978; Corkum 1978; Walton 1980; Ciborowski 1983; Kohler 1985), then delayed recovery of drift in relation to bottom density may indicate long-term disruption by pesticides of fundamental biotic interactions in stream ecosystems. The similar delay in recovery of drift observed here and in Dimond's (1967) study indicates a need for research into the long-term effects of pesticides on drift phenomena in lotic systems, research that also may shed light on the basic causes of stream drift.

Drift is much easier to collect than benthic samples in rivers such as the Souris. In fact, a different artificial substrate benthic sampling method used in our preliminary studies had to be abandoned because the samplers became coated by filamentous algae, creating an atypical habitat. Thus, perhaps drift rather than benthic samples should be used to measure stream recovery or to indicate water quality (Larimore 1974). In large, deep, turbid rivers where benthos sampling in the centre of the river is very difficult, the use of drift sampling to indicate recovery after an insecticide treatment merits further investigation. Benthic samples taken close to the river banks, a common practise in many studies involving the impact of a toxicant on the benthos of large rivers, is likely to be a poor indicator of effects near the centre of the channel where concentration of the chemical and ecological conditions may be completely different. However, the disadvantages in using drift to indicate water quality also should be borne in mind: the habitats from which individuals originate are not always known, and not all benthic species drift.

Conclusion

Although the invertebrate community of the treated riffle had recovered by the following year, the results of this study should be put into proper perspective when attempting to determine the impact of methoxychlor treatments on invertebrates downstream of a treatment site. First, far-downstream species would be exposed under different conditions than those immediately downstream from methoxychlor addition. Pesticide concentration would be attenuated as it moved downstream, so invertebrates would be exposed to the chemical at lower concentrations, but for a longer period. Since the toxicity of methoxychlor increases with increasing exposure time for most organisms (Sanders and Cope 1968; Merna and Eisele 1973; Anderson and DeFoe 1980), taxa in downstream sites would be exposed to the pesticide under chronic conditions and could be at higher risk. Also, because of its physicochemical properties, much of the pesticide would be adsorbed onto suspended solids in the water column, so its availability to filter feeders downstream of application would be enhanced (Sebastien and Lockhart 1981). Second, downstream recovery could be prolonged because of the greater distance from upstream sources of colonization, although tributaries could hasten recolonization. Third, multiple methoxychlor treatments, as carried out in some black fly larviciding operations in western Canada (e.g. Byrtus 1981, 1982; Fredeen 1983) may be more harmful to benthic invertebrates than a single application such as investigated here. Last, potential effects of the treatment on biotic interactions and functional processes such as energy transfer and nutrient cycling (e.g. Wallace et al. 1982, 1986) also have to be considered in any decision to use methoxychlor — or any other nonselective pesticide — for black fly control in a river system.

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APPENDIX A. Sample ANOVA table — comparisons of drift density data for the mayfly, *Caenis tardata*.

Source	*df*	SS	MS	*F*-value	Pr > F
Site	1	3.86	3.86	15.88	0.0163
Replicate (site) (error A)	4	0.97	0.24		
Date	6	53.32	8.89	37.20	0.0001
Site × Date	6	36.33	6.06	25.34	0.0001
(PreC[a] + 15 Jul 82T[b]) − (PreT[c] + 15 Jul 82C[d])	1	6.90	6.90	28.90	0.0001
(PreC + 21 Jul 82T) − (PreT + 21 Jul 82C)	1	10.86	10.86	45.45	0.0001
(PreC + 29 Jul 82T) − (PreT + 29 Jul 82C)	1	6.66	6.66	27.89	0.0001
(PreC + 17 Aug 82T) − (PreT + 17 Aug 82C)	1	4.09	4.09	17.14	0.0004
(PreC + 03 Aug 83T) − (PreT + 03 Aug 83C)	1	1.00	1.00	4.17	0.0523
Replicates (site × date) (error B)	24	5.73	0.24		
Total	41	100.22			

[a]PreC = pretreatment control site.
[b]15 Jul 82T = 15 July 1982 treatment site.
[c]PreT = pretreatment treatment site.
[d]15 July 82C = 15 July 1982 control site.

Random Movement and Orientation in Pink Salmon (*Oncorhynchus gorbuscha*) Migrations[1]

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Hiramatsu, K., and Y. Ishida. 1989. Random movement and orientation in pink salmon (*Oncorhynchus gorbuscha*) migrations. Can. J. Fish. Aquat. Sci. 46: 1062–1066.

The homing migration of pink salmon (*Oncorhynchus gorbuscha*) from the open ocean towards their natal rivers was studied by a mathematical model using data from tagging experiments. In this model fish migration was considered to be the resultant of fish orientation and random movement. The mean migration speed and dispersion coefficient (an index of random movement) evaluated from regression analysis were 19.6 km·d^{-1} and 739 km^2·d^{-1} for the North American group and 47.1 km·d^{-1} and 863 km^2·d^{-1} for the East Kamchatkan group, respectively. The results indicated that pink salmon migration has more oriented movement than had been suggested by a previous computer simulation by other workers. The results also indicated that there is a distinct difference in the migratory behavior of North American and East Kamchatkan pink salmon.

La migration des saumons roses (*Oncorynchus gorbuscha*) vers leur rivière natale a été étudiée au moyen d'un modèle mathématique à partir de données provenant d'expériences de marquage. Dans ce modèle, la migration des poissons a été considérée comme résultant de l'orientation des poissons et de leur déplacement au hasard. La vitesse moyenne de migration et le coefficient de dispersion (indice de déplacement au hasard) évalués à partir d'une analyse de régression s'établissaient respectivement à 19,6 km·d^{-1} et à 739 km^2·d^{-1} pour le groupe d'Amérique du Nord, et à 47,1 km·d^{-1} et à 863 km^2·d^{-1} pour le groupe de l'est du Kamchatka. Les résultats ont montré que la migration du saumon rose est davantage dirigée que ne l'avait laissé supposer les travaux antérieurs de simulation informatique effectués par d'autres chercheurs. Les résultats ont révélé également qu'il existe une différence marquée entre le comportement de migration du saumon rose d'Amérique du Nord et celui du saumon rose de l'est du Kamchatka.

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Various species of fishes migrate in the ocean. These migrations are neither completely straight nor completely random. It would be appropriate to consider fish migration as the resultant of the orientation and random movement as the first approximation (Jones 1959). On the one hand, Saila and Shappy (1963) proposed a weighted (or biased) random walk model for Pacific salmon migration. Their computer simulation indicated that the migration of Pacific salmon from the high seas to the vicinity of their natal stream may be accomplished with only slight homeward orientation. Quinn and Groot (1984), on the other hand, reexamined the biological assumptions of this simulation in light of current knowledge of Pacific salmon. They concluded that salmon homing migrations are highly oriented.

In this paper, random (dispersion coefficient) and orientation (mean migration speed) components in pink salmon migration from the open ocean towards their natal stream were evaluated from tag recovery data and compared with Saila and Shappy's (1963) simulation to ascertain the extent of random movement by homing salmon.

[1]An earlier version of this paper was submitted to the Annual Meeting of the International North Pacific Fisheries Commission, Anchorage, Alaska, 1986 October.

Materials and Methods

Model

The following model is assumed to describe the behavior of fish:

$$(1)\quad \begin{pmatrix} X(t) \\ Y(t) \end{pmatrix} = \begin{pmatrix} U_x \\ 0 \end{pmatrix} t + \begin{pmatrix} R_x(t) \\ R_y(t) \end{pmatrix}$$

where the X axis is the direction of orientation. In salmon migration it is the direction of the natal river (Fig. 1). U_x is the speed of movement along the X axis and R_x and R_y are random walks (or dispersion) along the X and Y axes, respectively. Thus, the first term is an orientation component and the second term is a random component of movement. By definition of the random variable;

$$(2)\quad E[R_x(t)] = E[R_y(t)] = 0$$
$$E[R^2{}_x(t)] = 2D_x t, \quad E[R^2{}_y(t)] = 2D_y t$$

where $E[\ ]$ is an average (or expectation), D_x and D_y are dispersion coefficients (Beverton and Holt 1957) in the X and Y axes, respectively.

According to this model, the probability distribution of fish $f(X,Y,t)$ is:

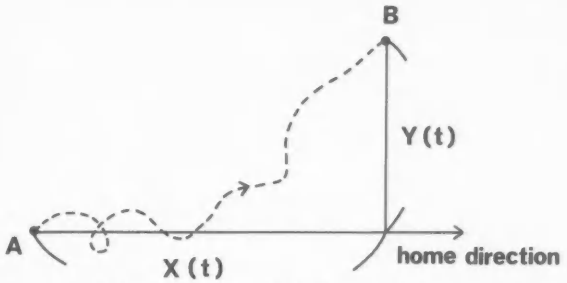

FIG. 1. Definition of $X(t)$ and $Y(t)$. Broken line indicates actual fish behavior. In tagging experiment: A = release point; B = recovery point; t = number of days between release and recovery.

$$(3)\quad f(X, Y, t) = \frac{1}{4\pi t\sqrt{D_x D_y}} \exp\left\{-\frac{(X - U_x t)^2}{4D_x t} - \frac{Y^2}{4D_y t}\right\}$$

(Appendix A). If the direction of orientation is known, U_x, D_x, and D_y can be estimated from tag recovery data using equation (3). Since the natal river of salmon caught in the open ocean is unknown, however, it is impossible to determine U_x, D_x, and D_y directly.

Thus, we considered the distance between points of release and recovery (distance traveled) which can be calculated from tag recovery data. Average distance traveled L is:

$$(4)\quad L = E[(X^2(t) + Y^2(t))^{1/2}] = E[(U^2_x t^2 + 2U_x R_x(t)t + R^2_x(t) + R^2_y(t))^{1/2}].$$

This relation between time and distance travelled is rather complicated and not linear. On the other hand, average squared distance traveled, L^2, is a much more simple function of time:

$$(5)\quad L^2 = E[X^2(t) + Y^2(t)] = U^2_x t^2 + 2(D_x + D_y)t.$$

Theoretically, the average migration speed U_x and a dispersion coefficient in two dimensions D $(=(D_x + D_y)/2)$ can be calculated from multiple regression relating average squared distance to time and squared time.

Saila and Shappy's Model

Saila and Shappy (1963) presented a weighted (or biased) random walk model to simulate the homing migration of Pacific salmon. In their model the pattern of step-lengths is described by a cardioid:

$$(6)\quad \mathbf{R} = R\cos\theta\mathbf{i} + R\sin\theta\mathbf{j}$$

where $R = P(1 + A\cos\theta)$, $\mathbf{i}$ and $\mathbf{j}$ are unit vectors in the X (homeward direction) and Y directions, respectively. R is the radius of curvature at any angle, θ (an angle measured in radians from the X axis), for the cardioid and A is a measure of directed movement versus undirected movement. A is a constant; θ and P are random variables.

The relation between equation (1) and this model is as follows. Let $\bar{P}$ be the average of P and σ^2 be the variance of P. The average migration speeds in the X and Y directions, U_x and U_y are:

$$(7)\quad U_x = E[R\cos\theta] = \frac{1}{2}\bar{P}A$$

$$U_y = E[R\sin\theta] = 0.$$

The dispersion coefficients in the X and Y directions, D_x and D_y are:

$$(8)\quad D_x = \frac{1}{2}E\left[\left(R\cos\theta - \frac{1}{2}\bar{P}A\right)^2\right] = \frac{1}{4}(\bar{P}^2 + \sigma^2)\left(1 + \frac{1}{4}A^2\right) + \frac{1}{8}\sigma^2A^2$$

$$D_y = \frac{1}{2}E[(R\sin\theta)^2] = \frac{1}{4}(\bar{P}^2 + \sigma^2)\left(1 + \frac{1}{4}A^2\right).$$

Details of the derivation of these equations are given in Appendix B.

When the length under consideration (for example, the distance traveled between release and recovery) is greater than each step length in this model, their random walk model is equivalent to equation (1).

Equation (7) and (8) show that σ^2, the variance of P, is an important factor which determines the D_x and D_y. Unfortunately, its value was not specified in Saila and Shappy's (1963) paper. If we let $\sigma^2 = \alpha\bar{P}^2$ (α is a constant), equation (7) and (8) can be solved for A and $\bar{P}$

$$(9)\quad A = 2\left(\frac{1 + \alpha}{4D/U_x^2 - 1 - 2\alpha}\right)^{1/2}$$

$$\bar{P} = \left(\frac{4D - (1 + 2\alpha)U_x^2}{1 + \alpha}\right)^{1/2}.$$

Hence, at $\alpha = 0$, A is minimum and $\bar{P}$ is maximum. The following analyses were restricted to this case.

Application to Tag Recovery Data

The average migration speed U_x and the dispersion coefficient in two dimensions D were calculated from pink salmon tag recovery data. Large numbers of Pacifc salmon have been tagged on the high seas and recovered near the coasts of Japan, Canada, the United States, and the Soviet Union. We analyzed groups of pink salmon which were presumed to have originated from North America (except for Western Alaska) (North American group) and from eastern Kamchatka (East Kamchatkan group). Data were classified into these groups by plotting geographic location of release and recovery. The general distributions of these groups are shown in Fig. 2 (after Takagi et al. 1981).

If the shortest distance between point of release and recovery crossed the land and was considered to be largely different from actual distance travelled, the data were excluded from the analysis. Moreover, we only analyzed data on salmon tagged from June 1, when the fish were assumed to be migrating homeward. Since the breadth of the ocean is finite, the net distance travelled over a long period is limited. Thus, for fish at liberty for long periods, travel may tend to be under estimated. We restricted our analysis to data on salmon at liberty for no more than 30 d before recovery. The edited data set consisted of 1770 North American coastal recoveries and 517 East Kamchatkan recoveries (coastal and off shore).

Since multiple regression analysis relating average squared distance to time and squared time was unstable in the sense that a small change in the data could cause a large change in estimates of U_x and D, the following tentative methods were used. A weighted (the inverse of variances around the regression line) linear regression through the origin between the number of days and the distance traveled was calculated and the slope was used

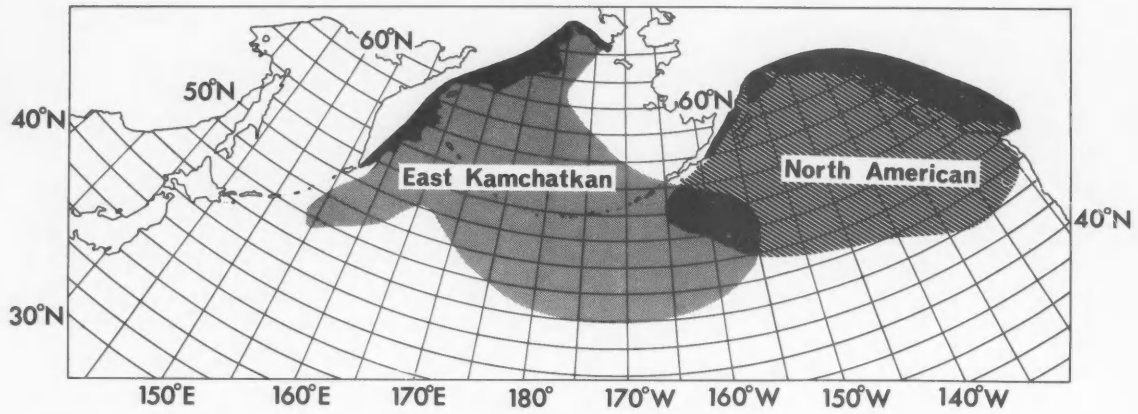

FIG. 2. General distributions of the North American and the East Kamchatkan pink salmon (after Takagi et al. 1981).

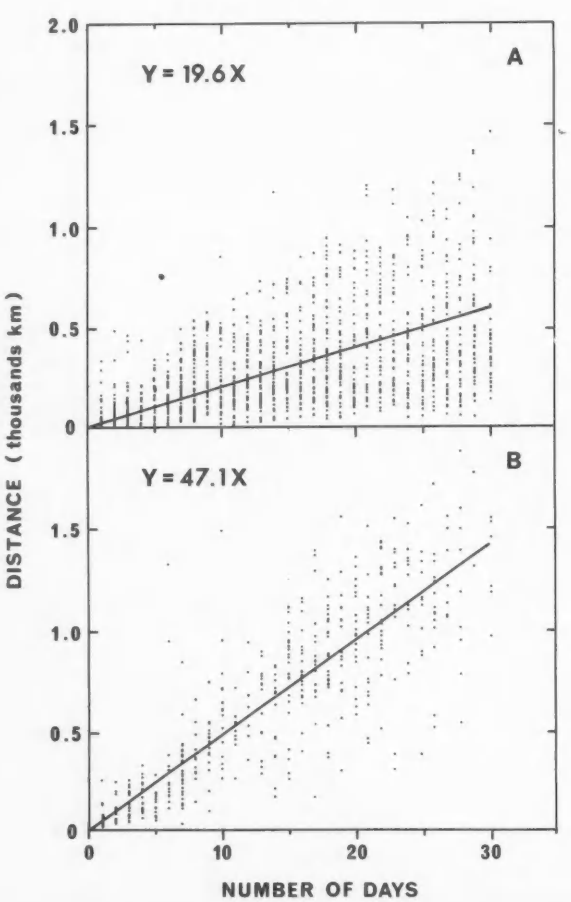

FIG. 3. Relation between the number of days and the shortest distances from release to recovery points. (A) the North American group, (B) the East Kamchatkan group.

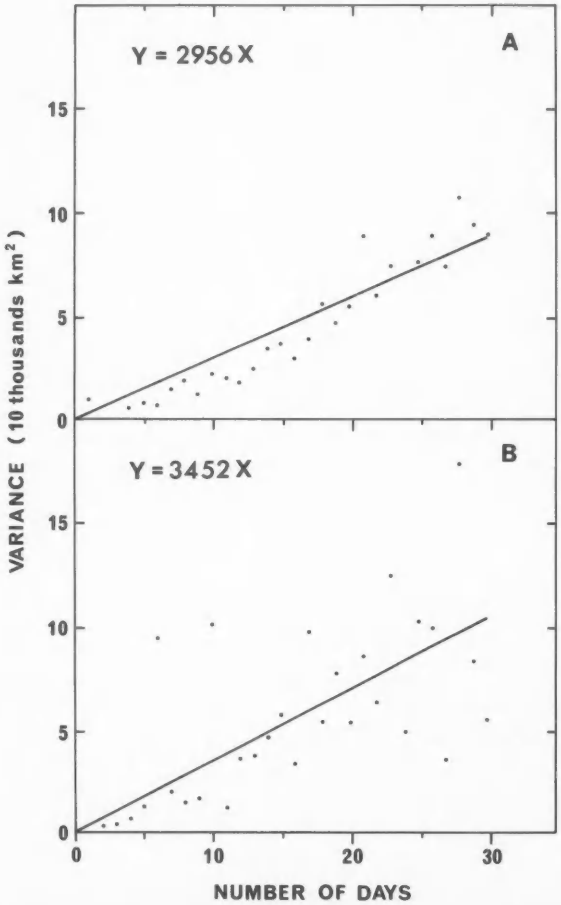

FIG. 4. Relation between the number of days and the variances from average distance travelled. (A) the North American group, (B) the East Kamchatkan group.

as an estimate of U_x (Fig. 3). Next, a linear regression through the origin between the number of days and the variances around the regression line was calculated and the slope was used as an estimate of $4D$ (Fig. 4).

Confidence limits for U_x and D were obtained by a bootstrap resampling procedure (Efron 1982). A sample was drawn randomly, with replacement, from the original data and U_x and D were calculated from this bootstrap sample. This procedure was repeated 10 000 times, yielding 10 000 bootstrap estimates. The bootstrap 95% confidence intervals were determined by the percentile method: the limits of the interval being the production value of 2.5 and 97.5% of the cumulative frequency curve of the bootstrap estimates.

Results

The results obtained were as follows:

North American pink salmon

$U_x = 19.6\text{km}\cdot\text{d}^{-1}$ $(19.0\text{–}20.3\text{km}\cdot\text{d}^{-1})$
$D = 739\text{km}^2\cdot\text{d}^{-1}$ $(675\text{–}809\text{km}^2\cdot\text{d}^{-1})$
$A = 0.77$ $\bar{P} = 50.7\text{km}\cdot\text{d}^{-1}$

East Kamchatkan pink salmon

$U_x = 47.1\text{km}\cdot\text{d}^{-1}$ $(45.7\text{–}48.6\text{km}\cdot\text{d}^{-1})$
$D = 863\text{km}^2\cdot\text{d}^{-1}$ $(667\text{–}1064\text{km}^2\cdot\text{d}^{-1})$
$A = 2.68$ $\bar{P} = 35.1\text{km}\cdot\text{d}^{-1}$

where the figures in parenthesis are 95% confidence intervals. These show that there is a distinct difference in travelling speed, whereas both groups disperse at a similar rate. To estimate the contribution of orientation and random movement to fish migration, the ratio of the distance of oriented movement to that of random movement after 30 d, that is $30U_x$ to $(120D)^{1/2}$, was calculated;

North American salmon	1.97
East Kamchatkan salmon	4.39

The results indicate that the contribution of oriented movement in the East Kamchatkan group is greater than that in the North American group.

Discussion

The value of A, the coefficient of directed versus undirected movement, is larger than that in Saila and Shappy's (1963) simulation ($A = 0.25$ and 0.3). This indicates that pink salmon migration is more oriented than they concluded and supports Quinn and Groot's (1984) conclusion numerically.

In their simulation the length of one step might be tens of kilometres. The results of a chum salmon tracking experiment (Ichihara et al. 1975), however, suggested that salmon change their swimming directions more often. It is reasonable to analyze salmon movements using equation (1).

Since tag recovery data did not result from random sampling, they may be biased. However, the effect of this bias may be diminished by using a large amount of data collected over the course of many years.

The actual fish behavior may be affected by such factors as their size, ambient water temperature, and the distribution of food (Takagi et al. 1981). All of the divergences from average distance travelled were assumed to be caused by randomness in this model, and thus the random component might be overestimated. However, since the relation between the divergence and these factors are unknown, it would be appropriate to analyze fish movement by assuming that the divergence from oriented movement results from random movement as the first approximation.

There is a clear difference in the migratory orientation between North American and East Kamchatkan salmon. This might be related to the fact that there is a difference in the migratory distance from the high seas to their natal stream between two groups (Fig. 2). On the one hand, the average migration speed of East Kamchatkan pink salmon (mean fork length is 45 cm) is near the maximum sustained speed at 10% fatigue level, about 53 $\text{km}\cdot\text{d}^{-1}$ (Brett 1982). On the other hand, that of North American pink salmon (mean fork length is 51 cm) is less than their maximum sustained speed, about 60 $\text{km}\cdot\text{d}^{-1}$. It seems that there is a difference in swimming energetics between them.

The method described in this paper provides a way to examine the fish behavior in the natural environment in cases where a large amount of tag recovery data is available. For further study, however, direct observation of fish behavior using techniques such as ultrasonic tracking (Stasko et al. 1973) is needed to determine the patterns of migration.

Acknowledgments

We are grateful to Dr. T. P. Quinn of Fisheries Research Institute, University of Washington, for his valuable comments in reviewing the manuscript. Material used in this paper was the magnetic tape recording recovery data (1956 to 1984) for salmon tagging experiments conducted by the scientists from the three countries; Japan, United States, and Canada, under the INPFC (International North Pacific Fisheries Commission).

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Appendix A: The Derivation of Equation (3)

The random variable R_y is assumed to obey the normal distribution with mean 0 and variance $2D_y t$. Hence, the probability distribution in the Y axis, $f_y(Y)$, is given by

(A1) $$f_y(Y) = \frac{1}{\sqrt{4\pi D_y t}} \exp\left(-\frac{Y^2}{4D_y t}\right).$$

The random variable R is assumed to obey the normal distribution with mean 0 and variance $2D_x t$. Thus, the distributional form of $U_x t + R_x$, $f_x(X)$, is the normal distribution with mean $U_x t$ and variance $2D_x t$:

(A2) $$f_x(X) = \frac{1}{\sqrt{4\pi D_x t}} \exp\left(-\frac{(X - U_x t)^2}{4D_x t}\right).$$

Since X and Y components are independent, the probability distribution in the two dimensions is given by

(A3) $$f(X, Y) = \frac{1}{4\pi t \sqrt{D_x D_y}} \exp\left\{-\frac{(X - U_x t)^2}{4D_x t} - \frac{Y^2}{4D_y t}\right\}.$$

Appendix B: The Derivation of Equation (7) and (8)

In Saila and Shappy's (1963) model, X and Y components of a step-length are given by

(B1) $$X = P(1 + A\cos\theta)\cos\theta$$
$$Y = P(1 + A\cos\theta)\sin\theta.$$

Since there is no relation between the random variables with different time steps, the migration speeds and the dispersion coefficients are given by

(B2) $$U_x = E[X]$$
$$U_y = E[Y]$$
$$D_x = E[(X - E[X])^2]$$
$$D_y = E[(Y - E[Y])^2]$$

where the expectations are the double expectation with respect to θ and P.

The average migration speed in the X direction U_x is

(B3) $$\begin{aligned} U_x &= E[P(1 + A\cos\theta)\cos\theta]_{P,\theta} \\ &= E[P]_P E[(1 + A\cos\theta)\cos\theta]_\theta \\ &= \bar{P}\,\frac{1}{2\pi}\int_0^{2\pi} (1 + A\cos\theta)\cos\theta\, d\theta \\ &= \frac{1}{2}\bar{P}A \end{aligned}$$

where $E[\ ]_x$ denotes the expectation with respect to x and $\bar{P}$ denotes the averge of P, $E[P]_P$. We made the assumption that the distributional form of θ is uniform. In the same manner, U_y is

(B4) $$\begin{aligned} U_y &= E[P(1 + A\cos\theta)\sin\theta]_{P,\theta} \\ &= E[P]_P E[(1 + A\cos\theta)\sin\theta]_\theta \\ &= \bar{P}\,\frac{1}{2\pi}\int_0^{2\pi} (1 + A\cos\theta)\sin\theta\, d\theta \\ &= 0. \end{aligned}$$

The dispersion coefficient in the x direction D_x is

(B5) $$\begin{aligned} D_x &= \frac{1}{2}E\left[\left\{P(1 + A\cos\theta)\cos\theta - \frac{1}{2}PA\right\}^2\right]_{P,\theta} \\ &= \frac{1}{2}\left\{E[(P(1 + A\cos\theta)\cos\theta)^2]_{P,\theta} - \left(\frac{1}{2}\bar{P}A\right)^2\right\} \\ &= \frac{1}{2}\left\{\frac{E[P^2]_P}{2\pi}\int_0^{2\pi}(1 + A\cos\theta)^2\cos^2\theta\, d\theta - \frac{1}{4}\bar{P}^2A^2\right\} \\ &= \frac{1}{2}\left\{\frac{E[P^2]_P}{2\pi}\left(\pi + \frac{4}{3}\pi A^2\right) - \frac{1}{4}\bar{P}^2A^2\right\}. \end{aligned}$$

Let σ^2 be the variance of P;

(B6) $$E[P^2]_P = \bar{P}^2 + \sigma^2.$$

Hence,

(B7) $$D_x = \frac{1}{4}(\bar{P}^2 + \sigma^2)\left(1 + \frac{1}{4}A^2\right) + \frac{1}{8}\sigma^2A^2.$$

In the same manner, D_y is given by

(B8) $$\begin{aligned} D_y &= \frac{1}{2}E[(P(1 + A\cos\theta)\sin\theta)^2]_{P,\theta} \\ &= \frac{1}{2}\,\frac{E[P^2]_P}{2\pi}\int_0^{2\pi}(1 + A\cos\theta)^2\sin^2\theta\, d\theta \\ &= \frac{1}{4}(\bar{P}^2 + \sigma^2)\left(1 + \frac{1}{4}A^2\right). \end{aligned}$$

Comparison of Actual and Potential Growth Rates of Brown Trout (*Salmo trutta*) in Natural Streams Based on Bioenergetic Models

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Preall, R. J., and N. H. Ringler. 1989. Comparison of actual and potential growth rates of brown trout (*Salmo trutta*) in natural streams based on bioenergetic models. Can. J. Fish. Aquat. Sci. 46: 1067–1076.

A ratio of specific growth rate to predicted maximum growth rate was employed as an ecological growth coefficient (EGC) in identifying major determinants of growth for brown trout, *Salmo trutta*, in natural streams. The coefficient may be more useful than specific growth rate when comparing trout populations from streams having diverse characteristics, since it accounts for the quantitative effects of stream temperature and mean trout weight. The maximum growth rate was generated by translating Elliott's bioenergetic equations into computer models applicable to fish weighing 5–300 g and to stream temperatures of 3.8–21.7°C. EQMAX is the simpler model and generates only maximum growth rate. TROUT estimates the maximum ration size, maximum growth rate, and a variety of bioenergetic parameters. The EGC for Age I+ trout ranged from 60 to 90% in three central New York streams. A relatively low EGC (30–60%) observed for Age II+ trout in one stream may have been due to the inefficiency of feeding on small invertebrates. Temperature appears to be a dominant feature governing trout growth in streams. The bioenergetic models may provide useful predictions of the effects of foraging on prey communities by brown trout.

Un rapport entre le taux de croissance spécifique et le taux de croissance maximale prévu a été utilisé comme coefficient écologique de croissance pour établir les principaux déterminants de la croissance chez la truite brune, *Salmo trutta* L., dans des cours d'eau naturels. Le coefficient peut être plus utile que le taux de croissance spécifique lorsque l'on compare des populations de truite de cours d'eau à caractéristiques variées, étant donné qu'il tient compte des effets quantitatifs de la température de l'eau du cours d'eau et du poids moyen de la truite. Le taux de croissance maximale a été obtenu en introduisant les équations bioénergétiques d'Elliott dans des modèles informatiques applicables à des poissons pesant entre 5 et 300 g et à des cours d'eau dont la température se situe entre 3,8 et 21,7°C. EQMAX est le modèle le plus simple et ne donne que le taux de croissance maximale. TROUT évalue la taille de la ration alimentaire maximale, le taux de croissance maximale et divers paramètres bioénergétiques. Le coefficient écologique de croissance pour les truites d'âge 1+ s'établissait entre 60 et 90 % dans trois cours d'eau du centre de New York. Un coefficient écologique de croissance relativement faible (30–60 %) relevé chez des truites d'âge II+ dans un cours d'eau peut avoir été causé par l'inefficacité de l'alimentation en petits invertébrés. La température semble être un facteur dominant régissant la croissance des truites dans les cours d'eau. Les modèles bioénergétiques peuvent fournir des prévisions utiles sur les effets de la recherche de nourriture par la truite brune dans les communautés de proies.

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Energy budgets have been developed for several species of fishes, including sockeye salmon (*Oncorhynchus nerka*) (Brett et al. 1969; Brett and Shelbourne 1975); walleye (*Stizostedion vitreum*) (Kelso 1972); largemouth bass (*Micropterus salmoides*) (Niimi and Beamish 1974); and yellow perch (*Perca flavescens*) (Solomon and Brafield 1972). Much remains to be learned, however, of the ways in which growth is governed under natural conditions where food supplies, temperature regimes, and numbers of competing individuals often fluctuate unpredictably. The extensive work by Elliott (1975a,b,c,d; 1976a,b,c) on feeding and growth of brown trout, (*Salmo trutta*) provides a rich base on which to develop our understanding of growth in nature. This species is particularly well suited to such work because of its wide distribution (MacCrimmon and Marshall 1968) and the availability of related studies on behavior and foraging ecology in stream populations (Ringler 1979, 1985; Ringler and Brodowski 1983; Bachman 1984; Bannon and Ringler 1986).

Growth of brown trout in lotic systems has been examined in relation to environmental factors including alkalinity, elevation, food supply, intraspecific and interspecific competition, and stream cover. McFadden and Cooper (1962) found that growth rate correlated positively with alkalinity in six Pennsylvania streams. Vincent and Miller (1950) and Purkett (1950) reported poor growth rates of brown trout at higher elevations of mountain streams. Ellis and Gowing (1957) determined that trout growth was limited by food in the less productive sections of a Michigan stream. Reduced growth was detected in sections of Michigan's AuSable River that had dense trout populations (Stauffer 1977); and Avery (1978) reported significant increases in growth of stocked trout following rotenone treatment of a Wisconsin stream.

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These studies indicate that complex interactions affect trout growth in streams. Comparison of growth rates among streams, however, does not clarify which factors are most important to determining growth, because streams often differ with regard to fish community structure and abiotic factors. McFadden and Cooper (1962), for example, examined the relationship of growth to alkalinity in six streams, but they did not examine temperature regimes. Since the streams of low alkalinity flowed through steep, shaded terrain, while those of high alkalinity flowed through broad, agricultural valleys, differences in their temperature regimes are very likely and growth rates would probably be less in the shaded mountain streams irrespective of alkalinity. Comparison of growth rates requires a standard that incorporates quantitative effects of different body weights and mean temperatures on the specific growth rate. If the effects of these two major factors are controlled, then growth can be examined in relation to food supply, alkalinity, competition or some other factor. The growth model used in this study generates such a standard.

We employed the bioenergetic equations of Elliott (1975c,d; 1976a,b,c) in a computer model that predicts the maximum growth rate of stream-dwelling brown trout. Model estimates (or simulations) of maximum growth provide a convenient basis for analysis of field estimates of growth rates. The maximum growth rate obtained in nature will usually be less than estimates obtained in the laboratory, where factors that reduce growth are eliminated. Laboratory estimates of maximum growth, however, can serve as a standard to which natural growth rates can be compared. The ratio of actual to predicted maximum growth ("Ecological Growth Coefficient" or EGC) provides a measure of ecological growth efficiency. Our study had two objectives:

1. To translate the bioenergetic equations of Elliott (1975c,d; 1976a,b,c) into a useful computer model,
2. to compare field estimates of trout growth in streams to the maximum growth predictions of the model.

Study Areas

Three streams in Onondaga County of central New York were selected for their variety of habitat and the existence of established populations of brown trout (Table 1).

Furnace Brook is a small, second order tributary of Onondaga Creek, with a total length of 4.4 km. The study site was a 70-m stretch which flows through a city park in Syracuse, NY (Fig. 1). Flood control measures have resulted in some channelization, and landscaping efforts have created a series of waterfalls and riffles. The banks of the stream are reinforced with large cobble set in cement. Undercutting of this cobble has provided much of the cover available to trout. The substrate consists largely of gravel and scattered cobble (4–6 cm diameter). Instream vegetation is sparse, and bankside vegetation consists largely of willows and a few planted shade trees.

Brown trout dominate the fish fauna in Furnace Brook. A small population of brook trout (*Salvelinus fontinalis*) is also present. The last recorded stocking of brown trout prior to this study was in 1975 (NYSDEC stocking records). Few trout old enough to have been stocked in 1975 were captured in this study, and all trout were assumed to have originated from natural reproduction. Fishing pressure during this study appeared to be very light. No anglers were observed and most park users expressed surprise that trout were in the study stream.

Nine Mile Creek (Fig. 1) is the largest of the three study streams with a total length of 36.2 km. It is the outlet of Otisco Lake, a Finger Lake southwest of Syracuse, and flows northeasterly to drain into Onondaga Lake. The 58 m study site on Nine Mile Creek was located 2 km downstream of the village of Marcellus. At this site, Nine Mile Creek is a third order stream. Below Marcellus, many springs enter the stream as the valley narrows and the gradient increases (2.1 $m \cdot 100\ m^{-1}$). These springs and the steep banks have an important effect on water temperature.

Nine Mile Creek is stocked annually with brown and brook trout. Brown trout are stocked in the fall as fingerlings and in the spring as yearlings (NYSDEC stocking records). Besides trout, only white sucker (*Catostomus commersoni*) were common at the sample site.

Nine Mile Creek was part of a 3-yr study of the effect of size limits on trout conducted by the New York State Department of Environmental Conservation. During 1978 and 1979, our sampling site averaged 5619 angler hours$\cdot ha^{-1} \cdot yr^{-1}$ and 6220 angler hours$\cdot ha^{-1} \cdot yr^{-1}$, respectively. Intense fishing pressure on Nine Mile Creek resulted in heavy fishing mortality of trout. A population and growth study, in conjunction with the creel census, estimated a 60% harvest of recruited year classes. Approximately half of the trout population was believed to have originated from natural reproduction (Engstrom-Heg and Hulbert 1983).

TABLE 1. Selected physical, chemical, and biological characteristics of three central New York streams.

Characteristic	Nine Mile Creek	Furnace Brook	Carpenters Brook
Site length (m)	58.0	73.0	103.0
Average width (m)	9.4	3.0	6.2
Average riffle depth (m)	0.50	0.33	0.67
Discharge ($m^3 \cdot s^{-1}$)	1.26	0.16	0.03
Gradient ($m \cdot 100\ m^{-1}$)	2.1	1.8	0.18
Bottom type	cobble–rubble	gravel–cobble	silt–gravel
pH	8.5	8.2	8.4
Conductivity (μS)	535	1090	1010
Total alkalinity (ppm $CaCO_3$)	197	203	248
Trout density (No.$\cdot ha^{-1}$)	1500	4939*	235
Trout biomass ($kg \cdot ha^{-1}$)	143	343*	32
Average trout weight (g)	95.6	87.7	137.4
Fishing pressure ($h \cdot ha^{-1}$)	5920**	slight	slight
Mean temperature 1979 (°C)	11.9	12.0	13.6
Mean temperature 1980 (°C)	12.2	13.5	19.1

* Average of 1979 and 1980 values.
**Average of 1978 and 1979 values.

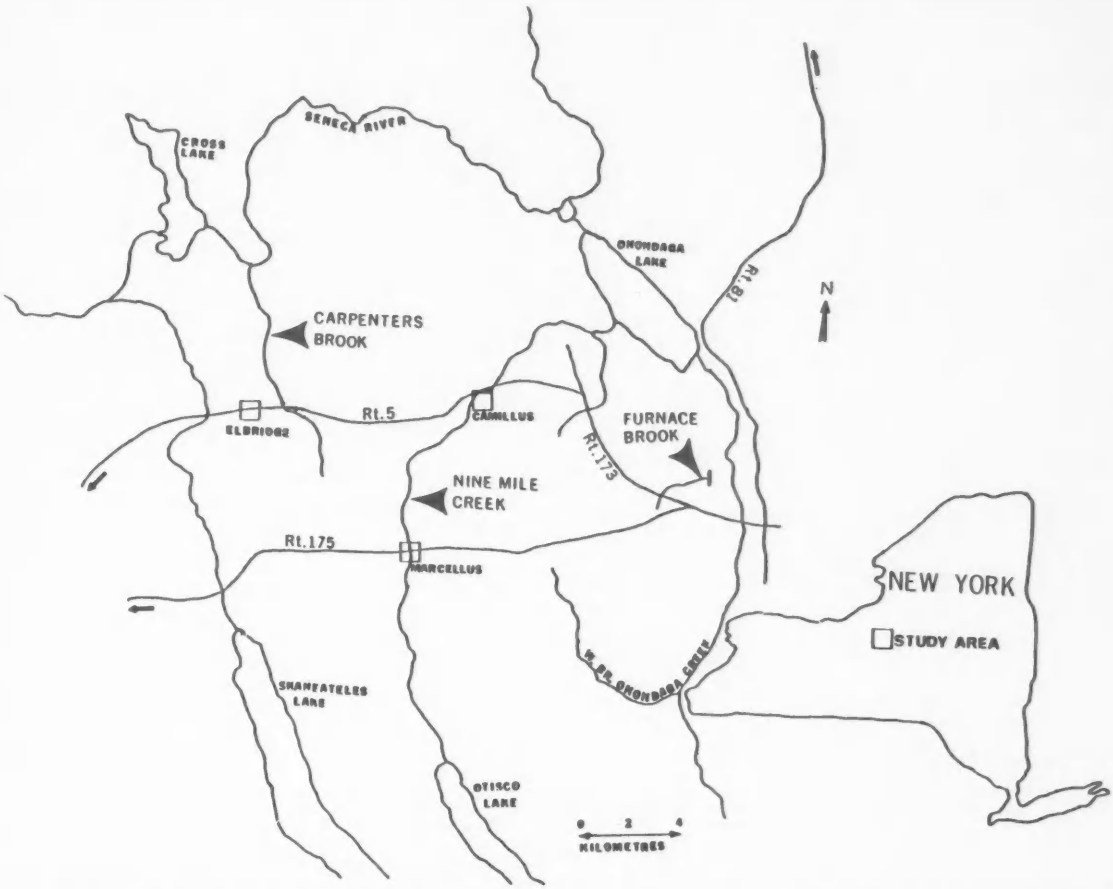

FIG. 1. Location of sampling sites on Furnace Brook, Nine Mile Creek, and Carpenters Brook in relation to selected topographic features. Geographic location of the general study area within New York.

Carpenters Brook, a lowland stream intermediate in size between Furnace Brook and Nine Mile Creek, originates in large springs, which are also utilized by a county fish hatchery. The 103-m sampling site was located 3.9 km above the stream's confluence with the Seneca River, near the village of Elbridge (Fig. 1). At the sampling site, Carpenters Brook is a third order stream.

The Carpenters Brook Fish Hatchery raises brown, brook, and rainbow (*Oncorhynchus mykiss*) trout. Escapement of fish may occur throughout the year, thus influencing stream populations. The stream is stocked annually in the spring with yearling brown trout. Populations of white sucker (*Catostomus commersoni*), common shiner (*Notropis cornutus*), and creek chub (*Semotilus atromaculatus*) dominated the fish community in terms of numbers and biomass.

Materials and Methods

Stream temperatures were measured using Taylor maximum–minimum thermometers, which were checked at least weekly from late June to November in 1979 and from mid-May to August in 1980. Mean temperatures based on one to two weekly readings of maximum–minimum thermometers seldom differ more than 1°C from means based on daily or hourly thermograph readings (Macan 1958; Edington 1966; Crisp and LeCren 1970; and Boon and Shires 1976). Similarly, in Nine Mile Creek we found close agreement (±1°C) between mean weekly temperatures calculated from thermograph records (May–July 1980) and means calculated from the maximum–minimum thermometers.

A Honda EM 400 electric generator (A.C.) producing 115 V at 3.5 A and equipped with two, fine-meshed electrodes was used for all field collections of trout. Three member crews were usually used for the electrofishing runs. Stunned trout were caught using scap nets and held temporarily in buckets or a wire mesh, submersible live car.

Total length (millimetres) of the trout was measured and scales were removed from an area just above the lateral line and below the origin of the dorsal fin. Nonregenerated scales were pressed in cellulose acetate using an Ann Arbor roller press. Annuli were identified by projecting the scales with a Bausch and Lomb Tri-Simplex microprojector (12–90×). Difficult scales were reread at later dates, and if no definite age could be determined, the fish was not used for growth estimates.

Trout were weighed on a Hanson balance accurate to ±2 g. Under field conditions, weighing unaesthetized fish, accuracy

could vary ±10 g. Because mass was a crucial measurement in this study, most trout were anesthetized using Tricaine Methanesulfonate (MS-222), which rarely caused mortality.

Trout were not marked or tagged in our study. Some hatchery trout in Nine Mile Creek were fin clipped by personnel of New York State Department of Environmental Conservation. We assumed that fin clipping of fish 175–250 mm in length would not affect their growth.

Population estimates of brown trout and other fish species in each stream were made in July 1979 using the two-catch method of Seber-LeCren (1976). Another population estimate was carried out in Furnace Brook in September 1980. Carpenters Brook was not reexamined in 1980 because no trout were captured by electrofishing in August. Nine Mile Creek was stocked with trout in the fall of 1980, before another population density estimate could be completed.

The chemical characteristics of each stream were measured in July and September 1979 and in May 1980. Two water samples from each stream were analyzed on these dates for total alkalinity, pH, and conductivity. Total alkalinity of the streams was estimated by titration with 0.01 M solution of sulfuric acid (Cole 1975). Conductivity was measured using a Model 31 YSI Conductivity Bridge (Yellow Springs Instrument Company). The pH of each stream was determined using a Corning Model 610 pH meter calibrated with standard pH solutions.

Fulton's Condition Factor (K) was used to indicate the relative "well being" of the individual trout on each collection date (Bagenal and Tesch 1978).

The EGC is a measure developed for use in this study. It is the ratio of the actual specific growth rate to the maximum specific growth rate predicted by the growth models:

$$(1)\quad \mathrm{EGC} = G\%_{\mathrm{obs}} \cdot G\%_{\mathrm{max}}{}^{-1} \cdot 100$$

where $G\%_{\mathrm{obs}}$ and $G\%_{\mathrm{max}}$ = the observed and maximum growth rates in percent increase wet body weight per day.

Model Development

The basic bioenergetic equation for the energy intake of an organism is (Warren and Davis 1967; Ricker 1971):

$$(2)\quad C = F + U + \Delta B + R$$

where C = consumption = total energy intake over time; F = feces = the portion of the ration not assimilated and which is egested; U = urine = the portion of the ration which is assimilated, but is excreted; ΔB = growth = the change in energy content; and R = respiration = the portion of the assimilated ration converted to heat, mechanical energy, and used in life processes.

Elliott (1976c) used this equation to detail the energy budget of brown trout. Multiple regression equations describing each component of equation (2) are presented in table 2 of Elliott (1976c). Body weight and water temperature are the driving variables in each of these equations.

The bioenergetic equations of Elliott (1976c) have been developed into a computer program (TROUT) which simulates the maximum possible growth rate over time for a brown trout living in a stream of a given temperature regime. TROUT is written in FORTRAN IV for mainframe computers and has been translated into MicroSoft BASIC for use on MS DOS compatible microcomputers. Required input data for TROUT are the initial weight and condition factor of the fish, its condition factor at the end of the timespan, and the weekly mean temperature regime. TROUT then iteratively calculates the weekly energetic losses and gains in kilocalories and sums these over the timespan involved. The model outputs the final weight, the maximum specific growth rate, and a variety of other information concerning the energy budget of the brown trout (Preall 1985).

TROUT was tested by comparing its maximum growth predictions to the experimental results of Elliott (1975c, Table 1). In the temperature range of 5.6–15.0°C, the model generates weight gains in excess of those observed by Elliott, with a maximum discrepancy of 15% between the values at 15°C (Preall 1985). At temperatures outside of this range, TROUT generated values equal to or below the experimental results. We attribute the systematic error in TROUT to low estimates for energy losses via respiration. Elliott (1976c) did not measure respiration directly and generated equations for this component based on values derived by simple difference when ΔB, C, F, and U were known.

In an effort to estimate the maximum weight gain more accurately a second program, EQMAX, was developed based on the following equation (Elliott 1975c, his equation 11):

$$(3)\quad W_t = [b_1 (a + b_2 T)\, t + W_i^{b_2}]^{1/b_2}$$

where t = time in days; T = temperature in Celsius; W_i = initial trout weight in grams; W_t = final trout weight in grams; a, b_1, b_2 = constants that vary with temperature.

EQMAX generated weight predictions that were within ±2 g of the experimental results of Elliott (1975c, Table 1) in the temperature range of 3.8–19.5°C.

EQMAX cannot be regarded as a better growth model than TROUT for all situations. EQMAX simulates only positive growth, and thus it has a narrower temperature range (3.8–19.5°C) than TROUT (3.8–21.8°C). TROUT is more realistic than EQMAX because it can model negative growth at temperatures above 19.5°C. Also, EQMAX does not include a variable for the condition factor of the trout. Elliott (1976a) has shown that the energetic composition of a trout's body can vary considerably with different condition factors and with increasing body weight. In natural situations, the condition factor of a trout changes seasonally. Only the TROUT model is programmed to accommodate changes in energy density which occur as a fish gains weight and its condition factor changes. We believe that TROUT supplies growth estimates as reliable as those of EQMAX when simulations of long-term growth involving variations in condition factor, relatively large weight gains, and temperatures greater than 19.5°C are being run.

Both TROUT and EQMAX adhere strictly to the experimental limits of Elliott (1975c; 1976a,b,c). These models are applicable only to brown trout weighing between 5–300 g. Each model is also limited to a specified temperature range (see above) and input data outside of these limits are converted to the nearest temperature extreme. Copies of the models are available from R. J. Preall.

Elliott worked only with immature trout in his feeding and growth experiments. The energetic losses associated with reproduction are, therefore, not included in TROUT. During the course of stream population studies investigators should determine if a significant proportion of fish below the 300-g weight limit are spawning.

Results

Stream Temperature

Mean weekly temperatues in 26 of 33 wk fell within the ideal range in Nine Mile Creek (Fig. 2a), suggesting a potentially

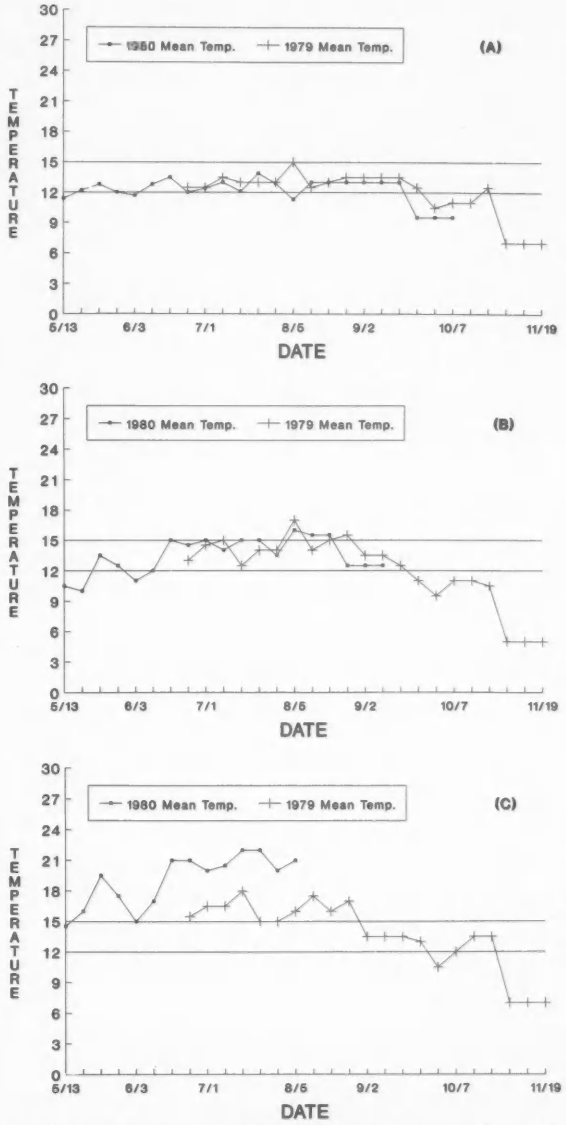

FIG. 2. Mean temperature profiles for three study streams. Composite of May–November temperatures for 1979 and 1980. Horizontal lines bracket an "ideal" mean temperature range for brown trout.

high growth rate for brown trout. Furnace Brook (Fig. 2b) was less homeothermic than Nine Mile Creek, with 21 of 33 weekly readings falling in the 12–15°C range.

Carpenters Brook had a poor temperature profile for brown trout growth and should probably be characterized as heterothermic (Fig. 2c). Weekly mean temperatures were quite different between years and even between consecutive weeks in the same year. Only 11 of 33 weekly mean temperatures were within the 12–15°C range. Most means (20 of 33) were higher than 15°C, especially in 1980. Early spring and fall were probably the only periods in which stream temperatures were conducive to rapid growth of trout in Carpenters Brook.

Age and Growth

Nine Mile Creek (Table 2) had larger trout of Age I+ and Age II+ than Furnace Brook and Carpenters Brook. Very few trout in Nine Mile Creek survived to Age II+ and beyond, probably as a result of heavy fishing pressure. Furnace Brook trout were of moderate size at each age, but exhibited a high rate of survivorship from Age I+ to Age II+. The mean weights of Age I+ and II+ trout in Furnace Brook were usually 50% lower than those achieved by trout of comparable age in Nine Mile Creek.

The mean length and weights at each age of trout in Carpenters Brook were highly variable. This is a result of small sample size and of differences in size between hatchery-raised and wild fish.

Model Results

The TROUT and EQMAX growth models provided theoretical growth rates that are readily compared with the actual growth rates of trout in the three study streams. Input data on stream temperatures, mean weights, and condition factors were utilized in the models to generate ecological growth coefficients for the intervals between consecutive sampling dates. An EGC value based on the entire collecting season was also generated. These EGC values provided a basis for comparing growth rates among streams of greatly differing temperature regimes and other growth-governing factors.

Nine Mile Creek

The growth of Age I+ brown trout was simulated for Nine Mile Creek in 1979 (Table 3). Results indicated that the EGC varied seasonally from 0–100%. On two of the EQMAX runs (1979-07-23 to 1979-11-19 and 1979-08-28 to 1979-11-19) the EGC was greater than 100%. Overestimates of EGC probably reflect sampling error in estimating mean weight. When the lower limit of the 95% confidence interval for the actual weight was used in the growth models, all EGC values fell below 100%. Therefore, the percentage deviation from 100% (9 and 16%), was not great enough in either case to invalidate EQMAX.

For the same two simulation runs that produced overestimates of the EGC by EQMAX, the TROUT model gave estimates of EGC well below 100%. This model is more realistic than EQMAX, but the simple EQMAX model was subsequently shown to have considerable predictive value. Therefore, unless otherwise stated, we have presented EGC as a range of these two values, with that based on TROUT given first (e.g. 74–95%).

EGC's of 0% were found for the dates 1979-06-30 to 1979-07-23 for Age I+ trout in Nine Mile Creek (Table 3). This evidently resulted from a negative specific growth rate during this period. The mean temperatures for these dates should have resulted in adequate growth (12–14 °C), so that the low coefficient resulted either from sampling error (unlikely here since $n = 36$ and $n = 48$ on the respective dates) or some other factor, such as a low food supply. Values of EGC for July–August and August–November were 74–95% and 95–116%, respectively. Overall, the coefficient for Age I+ trout in Nine Mile Creek in 1979 was 74–88%. High growth rates in the late summer and fall compensated for the relatively slow growth during early summer.

TABLE 2. Sampling date, length (millimetres), weight (grams), condition factor, and age for brown trout in Nine Mile Creek, Furnace Brook and Carpenters Brook in 1979 and 1980. The number in parentheses is the number of fish caught on each sampling date. Where sample size was large enough ±2 SE is included with the mean measurements.

	Nine Mile Creek		Furnace Brook		Carpenters Brook	
	I+	II+	I+	II+	I+	II+
Date	6/30/79	6/30/79	7/10/79	7/10/79	7/6/79	7/6/79
No. caught	(36)	(2)	(71)	(21)	(4)	(3)
Length	189.4±5.0	275.5	159.5±4.4	210.3±6.5	139.0±41.9	197.0±51.8
Weight	81.5±7.4	200.5	42.3±3.9	96.5±8.3	29.8±24.8	71.0±60.5
K	1.17±.04	1.13	1.00±.03	1.03±.03	0.94±0.14	0.81±.07
Date	7/23/79	7/23/79	—	—	7/21/79	7/21/79
No. caught	(48)	(2)	—	—	(2)	(7)
Length	195.4±4.8	234.0	—	—	176.5	214.3±15.1
Weight	79.3±6.8	150.5	—	—	45.5	82.9±19.1
K	1.03±.03	1.04	—	—	0.79	0.82±.05
Date	8/28/79	—	8/29/79	8/29/79	8/25/79	8/25/79
No. caught	(22)	—	(35)	(13)	(2)	(6)
Length	205.9±8.3	—	170.9±7.5	206.0±17.3	159.5	198.7±13.6
Weight	98.1±13.6	—	53.3±7.1	90.6±21.7	34.5	67.7±15.9
K	1.09±.03	—	1.02±.04	0.98±.03	0.85	0.84±.06
Date	11/19/79	—	11/19/79	11/19/79	11/19/79	11/19/79
No. caught	(9)	—	(33)	(10)	(3)	(1)
Length	231.1±.1	—	191.2±6.3	224.5±6.6	152.7±42.5	319.0
Weight	155.2±30.5	—	86.6±8.9	127.7±22.8	39.7±43.9	305.0
K	1.24±.11	—	1.20±.03	1.11±.07	0.89±.33	0.94
Date	5/27/80	5/27/80	5/20/88	5/20/88	5/27/80	5/27/80
No. caught	(29)	(5)	(5)	(15)	(1)	(5)
Length	190.5±6.6	217.4±13.2	148.8±15.6	200.3±9.7	150.0	200.4±21.7
Weight	84.2±8.4	111.5±18.1	41.0±17.8	97.7±15.0	35.0	86.4±25.4
K	1.19±.05	1.12±.05	1.17±.09	1.19±.04	1.04	1.04±.04
Date	7/28/80	7/28/80	6/27/80	6/27/80	—	6/27/80
No. caught	(19)	(1)	(17)	(27)	—	(5)
Length	218.6±10.1	210.0	172.9±7.6	200.1±9.0	—	211.2±27.6
Weight	121.2±18.4	112.0	56.1±7.9	89.3±9.7	—	94.4±35.0
K	1.13±.04	1.21	1.06±.07	1.09±.04	—	0.95±.04
Date	10/19/80	10/19/80	9/26/80	9/26/80	—	—
No. caught	(9)	(3)	(35)	(25)	—	—
Length	240.9±14.0	255.7	184.6±7.1	226.5±6.7	—	—
Weight	164.0±33.9	216.7	76.6±8.7	136.2±13.6	—	—
K	1.14±.07	1.30	1.17±.05	1.19±.04	—	—

A decrease in EGC early in the summer for Age I+ trout in Nine Mile Creek was not observed in 1980 (Table 3). The EGC for Age I+ trout in June–July was 83–98%. From late July to October the coefficient dipped slightly to 59–71%. Overall, the I+ trout in Nine Mile Creek in 1980 had an EGC of 72–83%, remarkably similar to the 1979 values.

The EGC's for Age II+ trout from Nine Mile Creek in 1980 are based on a small sample size (Tables 3). The limited data suggest that the season-long EGC for these fish is in the range of 78–90%, which is only slightly higher than that observed for Age I+ trout in the same stream.

A potential use for the TROUT and EQMAX growth models can be illustrated by using data for Age II+ trout from Nine Mile Creek (Table 3). On 1980-07-28 only one Age II+ trout was captured. A weight of 112.0 g was recorded for this fish, which is only 0.5 g more than the mean weight for Age II+ trout from this stream on 1980-05-27. It is likely that the July weight underestimates the true mean weight for that age class of trout. This would account for the very small EGC value of 1% for 1980-05-27 to 1980-07-28 and the overly large EGC values of 128–150% for 1980-07-28 to 1980-10-19. A more realistic mean weight for Age II+ trout in Nine Mile Creek on 1980-07-28 is the maximum weight range of 156.9–170.0 g generated by TROUT and EQMAX for the time span of 1980-05-27 to 1980-07-28. Thus, the TROUT and EQMAX models may serve as tools for predicting weight when small sample sizes yield unreliable results.

Furnace Brook

As in Nine Mile Creek, Age I+ trout in Furnace Brook in 1979 displayed seasonal differences in their ecological growth coefficients (Table 3). During July–August 1979 the EGC was 49–73%. From August–November the coefficient increased to 100–123%. The EGC for the entire sampling season (78–102%) was only slightly higher than that determined for trout in Nine Mile Creek. Thus, the trout in these two streams had virtually identical season-long EGC's, even though the trout in Nine Mile Creek were nearly twice the weight of trout in Furnace Brook in November (155 g versus 87 g, Table 2).

TABLE 3. Ecological growth coefficients for Age I+ and II+ brown trout from Furnace Brook, Nine Mile Creek, Carpenters Brook, and four streams of Avery and Hunt (1981). The value in parentheses in each column is the EQMAX estimate; the other value is from the TROUT growth model.

Date	Age I+	Age II+
Furnace Brook		
7/10–8/29/79	49(73)	0(0)
8/29–11/19/79	100(123)	82(103)
7/10–11/19/79	78(102)	38(50)
5/20–6/27/80	99(128)	0(0)
6/27–9/26/80	42(60)	65(92)
5/20–9/26/80	59(81)	40(54)
Nine Mile Creek		
6/30–7/23/79	0(0)	—
6/30–8/28/79	41(52)	—
7/23–8/28/79	74(95)	—
7/23–11/19/79	88(109)	—
8/28–11/19/79	95(116)	—
6/30–11/19/79	74(88)	—
5/27–7/28/80	83(98)	1(1)
7/28–10/19/80	59(71)	128(150)
5/27–10/19/80	72(23)	78(90)
Carpenters Brook		
7/6–7/21-79	549(863)	—
7/21–8/25/79	0(0)	—
8/25–11/19/79	19(27)	—
7/6–11/19/79	26(39)	—
Avery and Hunt (1981)		
Emmons Creek	81	
Radley Creek	92	
South branch Weddes Creek	60	
Mecan River	112	

The EGC's of Age II+ trout from Furnace Brook (Table 3) had a coefficient of 0% for July–August 1979. For August–November the EGC rose to 82–103%. The overall EGC for Age II+ trout in Furnace Brook in 1979 was 38–50%. This season-long EGC is lower than that calculated for Age I+ trout from Furnace Brook and for Age I+ and II+ trout from Nine Mile Creek.

In 1980, the trout in Furnace Brook again displayed seasonal differences in EGC (Table 3). For late May to June the coefficient was 99% for I+ trout. A decline in EGC (42–60%) occurred from late June to late September. The overall EGC for Age I+ trout in Furnace Brook in 1980 was 59–81%. Because the last sampling for Furnace Brook was on 1980-09-26, before the end of the growing season, it is possible that the overall EGC was underestimated.

Age II+ trout had quite different EGC values in comparison to the Age I+ trout in Furnace Brook in 1980 (Table 3). In late May to June, the Age II+ coefficient was 0% while that of the I+ trout was near 100%. From late June to late September the EGC ranged higher for Age II+ trout (65–92%) than for the I+ trout (42–60%). Overall, the II+ age class of trout in 1980 had a season-long EGC of only 40–54%, which was nearly identical to the 1979 values for Age II+ trout in Furnace Brook.

The following pattern seems evident for Furnace Brook and Nine Mile Creek. The EGC was high (80–100%) in the spring and fall, but was low (0–60%) in the summer. Limited evidence suggests that the mid-summer low EGC occurred sometime between June and August on each stream. Apparently, this low period can occur at different times for each stream and each year. At any given time, Age I+ and II+ trout may have different EGC's. On a season-long basis, however, the coefficient for Age I+ trout in both streams fell within the range of 60–90%. Age II+ trout in Nine Mile Creek also fell in this range, but Age II+ trout in Furnace Brook had substantially lower EGC's, in the range of 35–55%.

Carpenters Brook

Sample sizes from Carpenters Brook were very small in 1979, so our results (Table 3) must be viewed with caution. Yet, several things were learned from these analyses. The EGC for I+ trout from Carpenters Brook in 1979, which covers the entire sampling season, was low (26–39%, Table 3), and in contrast to the other streams no rise in EGC occurred during the fall months (1979-08-25 to 1979-11-19).

We calculated an EGC of 549–863% for Age I+ trout in Carpenters Brook during the interval of 1979-07-06 to 1979-07-21 (Table 3). Such unrealistically high percentages can only occur if the actual growth, as measured in the field, was much greater than the predicted maximum growth generated by TROUT or EQMAX. If this actually occurred, then the growth models are invalid. However, the sample sizes of trout were so small (4 and 2), that it seems more likely that accurate mean weights for the Age I+ trout were not determined. Either or both of the observed weights on the two collection dates may have been in error. It is important to recognize that the growth model results indicate that a theoretically impossible weight gain has been calculated from the field data. This was not readily apparent when examining the observed weight data. The growth models can therefore serve as a useful tool when analyzing weight gain data from small sample sizes. Similar excessively high EGC's were determined for Age II+ trout in Nine Mile Creek on 1980-07-28 to 1980-10-19 (Table 3). We regard these instances as being strong indicators of sampling error.

Carpenters Brook, Nine Mile Creek, and Furnace Brook each exhibited intervals when EGC's were 0% (Table 3), which occurs when a negative growth rate has been determined from the field data. It is possible for TROUT to simulate negative growth if the mean stream temperatures are sufficiently high. However, the mean temperatures for each data indicate that positive growth was possible.

An extensive literature search was made for data to supplement our work. Avery and Hunt (1981) studied four Wisconsin brown trout streams and published data compatible with our models. Mean lengths for Age I+ trout were converted to mean weights using the weight–length relationship determined for our study. Mean weekly temperatures were calculated from maximum and minimum weekly temperatures given in figure 14 (Avery and Hunt 1981) of their work. The EGC calculated for these four streams is provided in Table 3; these results are discussed below.

Discussion

The concept of maximum growth and the equations of Elliott (1975c) have been the stimulus for other recent studies (Edwards et al. (1979); Iwama and Tautz 1981; Condrey 1982; Craig 1982; Kerr 1982; Spigarelli et al. 1982; Jobling 1983; Stewert et al. 1983). Of these, Edwards et al. (1979) appears to be most directly comparable to our work. They employed a computer

growth model based on Elliott's (1975c) maximum growth equation which appears to be very similar to the EQMAX model used here. Working solely with Age I+ trout and monthly mean temperatures, they computed annual instantaneous growth rates for trout in 10 British streams. Edwards et al. (1979) concluded that actual growth rates ranged from 60 to 90% of the computed maximum for a broad variety of streams.

We found close agreement between the ecological growth coefficient for the season and the results of Edwards et al. (1979). Age I+ trout from Nine Mile Creek and Furnace Brook had EGC's in the 60–90% range, as did Age II+ trout in Nine Mile Creek. Three of the four streams studied by Avery and Hunt (1981) were found to have EGC's in this range.

Of 19 Age I+ trout populations analyzed here or by Edwards et al. (1979) only two fell outside an EGC range of 60–90%. In fact, many populations fell in the narrower range of 70–80%. Apparently, growth efficiencies for Age I+ trout are similar for a variety of streams, both in Great Britain and the United States.

Values of EGC outside the 60–90% range occurred for Age II+ trout from Furnace Brook, Age I+ trout from Carpenters Brook, and for the Mecan River of Avery and Hunt (1981). Inadequate sampling may explain the low EGC values found for Carpenters Brook, as only seven Age I+ individuals were captured. A lack of detailed information precludes making such inferences for the Mecan River (Avery and Hunt 1981).

Edwards et al. (1979) examined only the growth of Age I+ trout. Our study is evidently the first to analyze the growth of Age II+ fish from the standpoint of an ecological growth coefficient. In Furnace Brook, the season-long growth coefficients for Age II+ trout were considerably less than those for Age I+ trout (e.g. in 1979, Age II+ ranged from 37–50% in EGC while Age I+ ranged from 75–100%). In Nine Mile Creek, the two age classes had nearly identical ecological growth coefficients. This discrepancy warrants further examination.

The low season-long EGC's of Age II+ trout in Furnace Brook in 1979 and 1980 were caused by values of 0% during the early or mid-summer months. Minor decreases in the EGC were generally noted during the summer for all age classes of trout in the three study streams. High values in the late summer and fall usually compensated for these summer lows. The decrease was severe for Age II+ trout in Furnace Brook, however, and these fish failed to regain enough weight in the fall to bring their overall EGC to high levels.

Decreases in mid-summer growth rates have been noted by other investigators (Swift 1955; Ellis and Gowing 1957; Horton 1961; Sturgess and Moyle 1978; Moore 1982). Moore (1982) inferred that high summer temperatures were responsible for the decreased growth rate. The maximum growth rate for brown trout does decline when temperatures exceed 13°C, as Elliott (1975c) has shown, and his equation for predicting the maximum growth rate duplicates this decline. However, since the ecological growth coefficient is a ratio of observed growth rate over predicted maximum growth rate, variations in stream temperature are accounted for and do not directly influence the ratio estimate.

Swift (1955) demonstrated experimentally that peak thyroid levels occur during the summer months for Age III+ trout. He theorized that high thyroid activity can be linked to high metabolic rates and the onset of gonad maturation. Swift (1955) inferred that food rations during the summer could not supply enough energy to match metabolic requirements, so that trout would be forced to utilize body stores of fat. This explanation for growth declines may be applicable for sexually maturing trout, but it does not explain the decrease in EGC for immature I+ and II+ trout. The thyroid activity of Age I+ trout peaks in the spring (Swift 1955), when EGC levels are high. Ellis and Gowing (1957) and Sturgess and Moyle (1978) have stated that low food levels were responsible for the decrease in growth rate. A low level of food could certainly result in a decrease of EGC.

A recent study of benthic and drifting invertebrate abundances on Furnace Brook has shown that prey density reaches an annual low after emergence of mayflies (Ephemeroptera) in late May and June (Bannon and Ringler 1986). The density of benthic invertebrates following these hatches remained high, but the average size and weight of these potential prey items were reduced. Thus, it is likely that limited food availability is responsible for the decrease in EGC during the summer for Age II+ trout in Furnace Brook. An explanation is still required, however, for the disparate effects of this decrease in available food on Age I+ versus II+ trout. At the same time that Age II+ trout were experiencing negative growth rates, Age I+ trout had EGC's of 48–73% in 1979, and 100% in 1980.

One explanation for the disparate effect is based on the time required to obtain a maximum ration. Elliott (1975a) found that the amount of food eaten and satiation time for a maximum ration were dependent on body weight and water temperature. Thus, a 300-g trout requires an hour to reach satiation at 7°C (consuming 556 mg dry weight of *Gammarus*), but 3 h at 18°C while consuming 1400 mg (Elliott 1975a, his equation 3 and 6). Elliott's feeding and growth experiments were based on *Gammarus* or other small invertebrates as a food source. Feeding behavior of brown trout requires visual detection of the prey item and a response time dependent on the duration of the approach, attack, and handling of the prey (Ringler 1979, 1983; Bannon and Ringler 1986). Because the size and energy content of some invertebrates such as mayflies and midges is considerably smaller than that of *Gammarus*, a significant portion of a large trout's time may be spent in foraging. Higher temperatures also increase foraging time, because rapidly rising metabolic costs force trout to consume larger meals.

Trout cannot allocate all of their time to foraging. Feeding activities entail risk through predation, especially during the daylight hours (Alexander 1979). Disturbance during feeding may alarm trout and cause them to seek shelter or otherwise alter the feeding pattern (Bachman 1984). Dill (1983) found that many fish species decrease their foraging activity in an adaptive response to the risk of predation. Thus, even if abundant food is available, a trout may have a difficult time achieving its maximum ration. The low water levels and clarity of streams like Furnace Brook in summer presumably increase the risk of sustained feeding. Achieving a high ecological growth coefficient during the summer months must be difficult, therefore, especially for larger trout. This may explain our finding that Age II+ trout had a lower EGC's than Age I+ trout in Furnace Brook during the summer. Age II+ trout will be at an increased disadvantage when prey items are of small size, since this would necessitate even longer feeding times. Subsequent work has shown that most prey consumed by brown trout in Furnace Brook are well below a theoretical optimum size (Bannon and Ringler 1986).

High trout population density and biomass have been generally regarded as detriments to rapid trout growth (McFadden and Cooper 1964; Frost and Brown 1967; Stauffer 1977; Backiel and LeCren 1978). The results of this study and of Edwards et al. (1979) do not agree with the assumption of density-

dependent growth. Furnace Brook had a trout population density nearly 3.5 times higher than in Nine Mile Creek (and one of the highest reported in the literature), yet the EGC values for Age I+ trout in each stream were identical. We conclude that the difference in specific growth rates in these streams was due largely to differences in thermal regimes. The identical EGC values indicate that the trout in both streams achieved the same proportion of their respective maximum possible growth rates. High trout density in Furnace Brook did not appear to affect the EGC. Similarly, the EGC ranges calculated for Age I+ trout in all 10 British streams (Edwards et al. 1979) were virtually the same, yet it is likely that population densities and biomasses differed widely among these streams. Temperature would appear to be the dominant feature governing trout growth.

An environmental factor not examined in this study was food availability. An extensive survey of benthic and drifting invertebrate densities, coupled with a diet study for the trout in each stream, was considered beyond the scope of this study. Surprisingly, these tasks may prove to be unnecessary in some applications. The remarkable similarity of EGC's for Age I+ trout from 17 streams worldwide, which almost certainly have different food availabilities, suggests that this factor had little detectible influence on growth, once temperature and fish size are taken into account (i.e. on EGC). Edwards et al. (1979) compared growth efficiencies of food "poor" Scottish highland streams to the "rich" chalk streams of southern Britain. They found that fish in highland streams had higher growth efficiencies (~80%) than the chalk streams (~70%). Our findings for Age I+ trout from Furnace Brook and Nine Mile Creek concur with Edwards et al. (1979). It is possible, however, that Age II+ trout in Furnace Brook had low EGC's due to an inadequate food supply, and further work on this factor is needed. Of particular interest would be studies comparing growth in streams with major differences in prey size distributions.

The computer program TROUT may be used to study interactions of brown trout with stream invertebrates or other prey. TROUT can output the maximum daily ration in calories for a fish of known weight under a particular temperature regime. If the average weight of an age class of brown trout and the population size are known, the daily ration of the population can be calculated, and this summed to yield a monthly or yearly ration estimate. If the percentage of a food item in the diet has been estimated, that percentage multiplied by the ration size yields the calories of that food item (e.g. Cummins and Wuycheck 1971) consumed per day, month, or year. Similarly, the mean weight of a prey organism can be used to estimate the number of organisms eaten per unit time. Comparison of this value to estimates of prey density would prove useful in assessing the impact of foraging by brown trout on invertebrate production. Such an analysis would be especially important in studies of lotic trout populations at different densities or age/size structures, and seems to complement the work by Stewart et al. (1983) in lake ecosystems.

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LETTERS AND COMMENTS/ LETTRES ET COMMENTAIRES

Comments on "Dispersal of *Homarus americanus* larvae in the Gulf of Maine from Brown Bank" by G. C. Harding and R. W. Trites

I question Harding and Trites (1988) conclusion that the offshore areas are the major source of reproductive effort for the lobster population off Southwestern Nova Scotia, and its implication that the offshore is the major source of recruitment to the much larger inshore fishery. They base their conclusions on incorrect estimates of egg production, and larval production values of questionable significance. I will review three of the paper's major problems: (1) the use of an inappropriate definition of inshore and offshore areas, which inflates the size of the offshore; (2) errors in egg production calculations which overestimate offshore and underestimates inshore egg production; and (3) the inappropriate use of Stasko and Gordon's (1985) larval data.

Harding and Trites (1988) used a new definition for inshore and offshore, defining the inshore as all areas with a depth of <20 m (maximum of 17 km from the coast). The authors did not supply data to support their new definition, nor did they relate it to previously used definitions or existing management units. Previously used definitions of the inshore lobster grounds, based on known distributions of the inshore fishery are: (1) Wilder (1970) defined the traditional inshore area as depths less than 55 m (up to 40 km from the coast); (2) Miller et al. (1987), in an overview of the lobster resource in the Scotia-Fundy area, defined inshore as areas within the 46 m contour (up to 38 km from the coast; and (3) Sharp and Duggan (1985) found from an aerial survey that though inshore fishing effort was concentrated within the 37-m contour (up to 35 km from the coast) it did extend out to the 100-m contour (up to 70 km from the coast). The inshore management area extends out to the offshore boundary line approximately 92 km from shore (Pezzack and Duggan 1985).

The area between the 37- or 46-m depth contour and the offshore fishery is fished by inshore vessels and is referred to as the middle ground or midshore fishing area. The relationships between the middle ground lobsters and the coastal or offshore lobsters are unclear (Pezzack 1983, 1987). The middle ground should be treated as a separate area and not grouped with the offshore fishery of the continental slope or deep basin areas.

Harding and Trites (1988) definitions result in an overestimation of the offshore area by ignoring the existence of a separate middle ground. Misunderstanding could result if the data presented are interpreted as representing the actual inshore and offshore fisheries or lobster distributions. If their conclusion were accepted it would have a significant impact on existing management strategy.

The second problem I have with the paper, is that the egg production values are incorrect, being too high for the offshore and too low for the inshore. Firstly the authors used incorrect data: (1) offshore landings are inflated by 77%, through the inclusion of Canadian offshore landings from Georges Bank, even though Georges Bank is not discussed in the paper; (2) the correct mean carapace length for offshore berried females is 124 mm, which has 40% fewer eggs per female then the 145-mm size used; (3) the correct mean carapace length for inshore berried females is 103 mm, which has 11% more eggs then the 100-mm size used; (4) summer values for the percent females berried should be 2.5% inshore (range 1-[illegible]) rather then 2%, and 12% (range 5–22%) offshore, rather than 19% (Campbell and Pezzack 1986). Estimates of the percent of females berried are too low for the inshore areas, in part because they were based on winter data while the offshore were based on summer data. In both areas the percentage of females berried is higher in summer than winter.

The authors were also incorrect in suggesting that the proportion of berried females, offshore may be up to 60% and that multiple extrusion of eggs, in successive years, could be the cause. The data cited are fall surveys on the shallow area of western Browns Bank (Pezzack 1983) which do not represent the stock as a whole. These data showed an absence of both males and nonberried females on the Bank suggesting a difference in catchability or patterns and timing of migrations. Furthermore tagging studies have not shown that successive year egg extrusions are common in the offshore areas (D. S. Pezzack, unpubl. data).

Harding and Trites (1988) also used an incorrect method to estimate the number of berried females in the population. They estimated this by calculating the total weight of berried females in the population then dividing by the weight of the mean length berried female (G. C. Harding, pers. comm.). But their estimate of the total weight of berried females was wrong because they used values based on numbers of lobsters (percent mortality, percent female, and percent of females berried) and not weight, to convert the weight of landed catch to weight of berried females in the population.

Using the correct values and method, the ratio of inshore eggs to offshore eggs is 1.5 to 1 rather than 0.2 to 1, reported by Harding and Trites (1986). Even using the maximum values of percentage of females berried (4% inshore and 22% offshore) the ratio is 1.4 to 1. Campbell and Pezzack (1986), using a more detailed computational method, determined that sufficient egg production existed in the inshore areas to allow local recruitment. The inshore areas support a much larger population then the offshore, with more, though smaller berried females, and a larger total egg production.

The third major problem is Harding and Trites' (1988) larval production calculations, which were based on published summaries in Stasko and Gordon (1983). The use of published summaries, rather than the raw sample data, are inappropriate for the quantitative comparisons the author attempted, since true means, variances, or confidence limits of their estimates cannot be determined.

I question their use of the mean catch per station to calculate larval production, without considering the confidence limits of

their estimate. Previous lobster larval work has shown larval distribution to be patchy and that confidence limits around the mean catch can be very large. Harding et al. (1982) reported standard deviations of 75% of the mean, in St. Georges Bay, using a tighter grid and larger net. From the Stasko and Gordon (1983) report, I calculate that the standard deviation of the mean number of larve/station (untransformed data) is up to four times the mean catch. The distribution of larval numbers/station is highly skewed with many zero catches and a few very large catches. In each offshore survey, 40–50% of the total stage 1 larvae were taken at a single station, and 70–80% from only 3 of the 28 stations. The arithmetic mean used is biased in small samples of highly skewed data, like those presented by Harding and Trites (1988). Delta, log normal, or negative binomial distribution would better describe the data (Cassie 1962; Green 1979; Smith 1981; Pennington 1983). Without confidence limits or statistical testing, it is impossible to determine if their production values have any significance.

Furthermore Harding and Trites (1988) gave no details on the methods used to convert the summary data of Stasko and Gordon (1983) to their final production values. Was the data corrected for larval duration at different temperatures (Scarratt 1964; Fogarty et al. 1984), and how were missing samples treated (18% of offshore stations dropped in 1978, over 30% of the offshore stations missed on some 1977 cruises)? Information on these calculations should have been included.

The authors also pooled the 2 yr (1977, 1978), and the three inshore and the two offshore areas in which Stasko and Gordon (1983) summarized their data, obscuring significant differences which existed within the areas and between years. The pooling of the 1977 and 1978 offshore data can further be questioned because the sampling design changed from a 28 station day and night sampling in 1977 to a 23 station daylight only survey in 1978. With our present knowledge of lobster larval diurnal migrations (Harding et al. 1987), it is clear that the 2 yr are not comparable.

Finally the surface area of the inshore and offshore, used to expand the larval catches and estimate total larval numbers, are inappropriate for reasons already discussed. By combining Stasko and Gordon (1985) offshore north and offshore south areas, which correspond closely to the middle ground and offshore lobster concentrations (Pezzack 1983) and the commercial fishery, Harding and Trites (1988) greatly inflated the apparent offshore production while ignoring the existence of a separate middle ground.

A stock recruitment relationship has not been shown to exist for lobsters and it is doubtful if a relationship exists between adult stock size, egg numbers, or larval number and future recruitment to the fishery which could be applied to different areas. Higher post larval morality in the less favorable offshore habitat, may mean that more larvae are required to support the smaller offshore population. The lack of a simple stock recruitment relationship is illustrated by the sharp rise in landings in recent years. The lobsters which make up the present landings, the highest since the turn of the century, originated during a period of near historic low landings in the mid 1970's.

I believe that contrary to the authors conclusions that "... three separate estimates indicate that the offshore contributes between 80 and 97% of the larval recruits in the entire southwestern Nova Scotia region...," a second look reveals that the inshore produces 1.5 times more eggs than the offshore, that the larval production values were based on small and highly variable catches, and that the higher larval numbers offshore were to a large extent the result of the definitions of inshore and offshore used — D. S. Pezzack, *Department of Fisheries and Oceans, Invertebrate Fisheries and Aquaculture Division, P.O. Box 550, Halifax, N.S. B3J 2S7*

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A Further Elaboration on "Dispersal of *Homarus americanus* Larvae in the Gulf of Maine from Browns Bank," in Response to Comments by D. S. Pezzack

Inshore–Offshore Definition

The definition of inshore and offshore lobster grounds that we adopted is not new but corresponds closely with the definition used by Stasko and Gordon (1983) which forms, in large part, the basis for our article. In their report about the seasonal distribution of larval lobsters off southwestern Nova

Scotia, Stasko and Gordon (1983) define inshore stations as those occurring within 3.9 km from shore, except in the Trinity Ledge area where the inshore extends to 9.3 km (see Fig. 1). We decided to use the 20-m depth contour to delineate this inshore region because it includes all of Stasko and Gordon's (1983) inshore stations yet extends the area to represent much of the inshore, small boat, lobster fishery (Fig. 1). Wilder (1970) wrote that "over the years, the inshore fishermen of southwestern Nova Scotia have progressively fished farther offshore. Some now make substantial catches on Lurcher Shoal, and on the Seal Island grounds, 15–20 miles from port." Both these offshore shoal areas are included in our definition of inshore lobster grounds (Fig. 1).

On the other hand, fishermen from southwest Nova Scotia have been setting some traps, seasonally, down to 55-m depth near these offshore shoal areas since the turn of the century (Prince 1899; Halkett 1916). Following the establishment of a separate offshore fishery, >50 nautical miles (~92 km) from shore, and the widespread decline of Maritime lobster stocks in the 1970's, there has been some concern that traditional inshore fishermen of southwestern Nova Scotia have been maintaining the level of their catch by trapping previously unfished deeper waters (Pringle et al. 1983). Aerial surveys of lobster trap buoys in the region during the 1983–84 season have shown that deeper sets (37 to 55 m) occurred more frequently west towards Lurcher Shoal than south of Seal and Sable Islands (Sharp and Duggan 1985). Buoy densities of 10 to 50 km^{-2} were observed closest to shore, with a sharp decline from 10 to <1 buoys·km^{-2} between 30–40-m depth contours off Seal Island and between 30–55-m depths towards Lurcher Shoal. A low level of fishing effort extended out to German and Browns Banks but these buoys represented trawls of up to six traps compared with the two to three traps per buoy inshore (Sharp and Duggan 1985). There are clearly commercial quantities of lobsters caught at greater depths from small inshore boats than the inshore definition we have adopted indicates, as Pezzack points out, even if this cannot be quantified separately at present (see Miller et al. 1987).

We were concerned primarily with the recruitment of planktonic larvae, and it has long been known that fecund females migrate to shallower water where the temperature is higher to hatch and release their offspring. Prince (1899) wrote about lobsters in southwest Nova Scotia "great schools pass the winter at depths of 40 or 50 fathoms (70 to 90 m); but during the warm summer months they move into shallow water, 2 to 10 fathoms (4 to 18 m), where the females ripen their eggs and hatch them out." Recently Campbell (1986) documented that ovigerous females nearby off Grand Manan underwent a 20-km or more seasonal migration from less than 20-m depth in summer and fall to 200 m or more during winter and spring. Well documented seasonal migrations of larger, deep water lobsters occur from the continental slope and canyons to shallower waters in summer on Georges Bank (Cooper and Uzmann 1971; Uzmann et al. 1977) and Browns Bank (Campbell and Stasko 1985; Pezzack and Duggan 1986). Similarly deep water lobsters are known to migrate from Jordon and Crowell Basins in the Gulf of Maine to shallower waters on German, Browns, and Georges Banks and further inshore towards Maine and southwest Nova Scotia (Anon. 1985; Duggan and Pezzack 1985; Campbell and Stasko 1985; Pezzack 1987).

In summary, summer movements of adult lobsters off southwestern Nova Scotia are directed towards shallower waters usually <20-m depth in inshore waters, or to less than 100 m on offshore banks. This dichotomy in adult female, summer distribution is supported by the distribution of first stage larvae derived from the St. Andrews neuston surveys (Fig. 1). All areas with greater than five larvae caught per station are shaded in Fig. 1. Few larvae were caught between the Browns and German Banks and the inshore region. The band of larvae found offshore between Browns Bank and Lurcher Shoal could not be contoured on the western side because it was located on the edge of the survey grid (Fig. 1). However, we know from our own sampling between Browns and Georges Bank in 1983 and 1986 that lobster larvae are rarely, if ever, released in deep water over the open Gulf of Maine.

Our choice of terms was perhaps unfortunate, in that fisheries management people have different meanings for inshore and offshore lobsters. If future research confirms the geographic separation of larval release and spawning based on water depth and proximity to deep water, the definition used by Stasko and Gordon (1983) will make more sense for further ecological interpretations of the lobster populations.

Larval Production from Estimates on Berried Females

There are a great number of uncertainties involved in calculating the number of larvae produced inshore and offshore from estimates of fecund female lobsters. We have to use the lobster landings, together with some scaling factor for mortality, as an estimate of population size. The Canadian landings on Georges Bank were included in the offshore (>50 *n* miles) Scotian Shelf and Browns Bank landings. We think there is clear evidence for some dispersal of larvae from the Georges Bank gyre towards southwestern Nova Scotia (Harding et al. 1983; G. C. Harding, unpubl. data), although the majority of larvae produced on Georges will remain and settle there. Georges Bank is an even more prolific source of offshore larvae than the German–Browns Bank region (G. C. Harding, unpubl. data 1983, 1986–88). It is impossible to place a value on either the contribution of dispersed or retained larvae from Georges Bank, but the lobster landings in the American sector are greater (1977: 718t; 1978: 1164 t) than those found in the entire Canadian offshore fishery (1977: 635 t; 1978: 685 t) (Fogarty et al. 1982; Statistics Canada 1977–78).

The definition we have adopted for the offshore places an additional complication on estimating the breeding population because the lobsters trapped under the Browns Bank to Lurcher Shoal are reported together with the inshore landings. Thus we have an average population of 920 (+) t lobster near Browns Bank in 1977 and 1978 (0.7 annual mortality rate, Campbell and Pezzack 1986) together with unknown contributions to our offshore population from the German Bank region and the much larger population on Georges Bank.

A second contentious issue in calculating potential recruitment from adult stock is the number of fecund females present in different areas. Stasko (1980) reported that <1% of the female population bear eggs from inshore southwest Nova Scotia landings compared with 19% from the offshore landings. However, the inshore fishery, which provides much of our inshore population statistics, is closed from June through to the last Tuesday in November, and this coincides with the annual migration of fecund females into and out of shallower waters. The offshore fishery is open year round. More recently Campbell and Pezzack (1986) have reported the percentage egg bearing of the total female population from experimental trapping

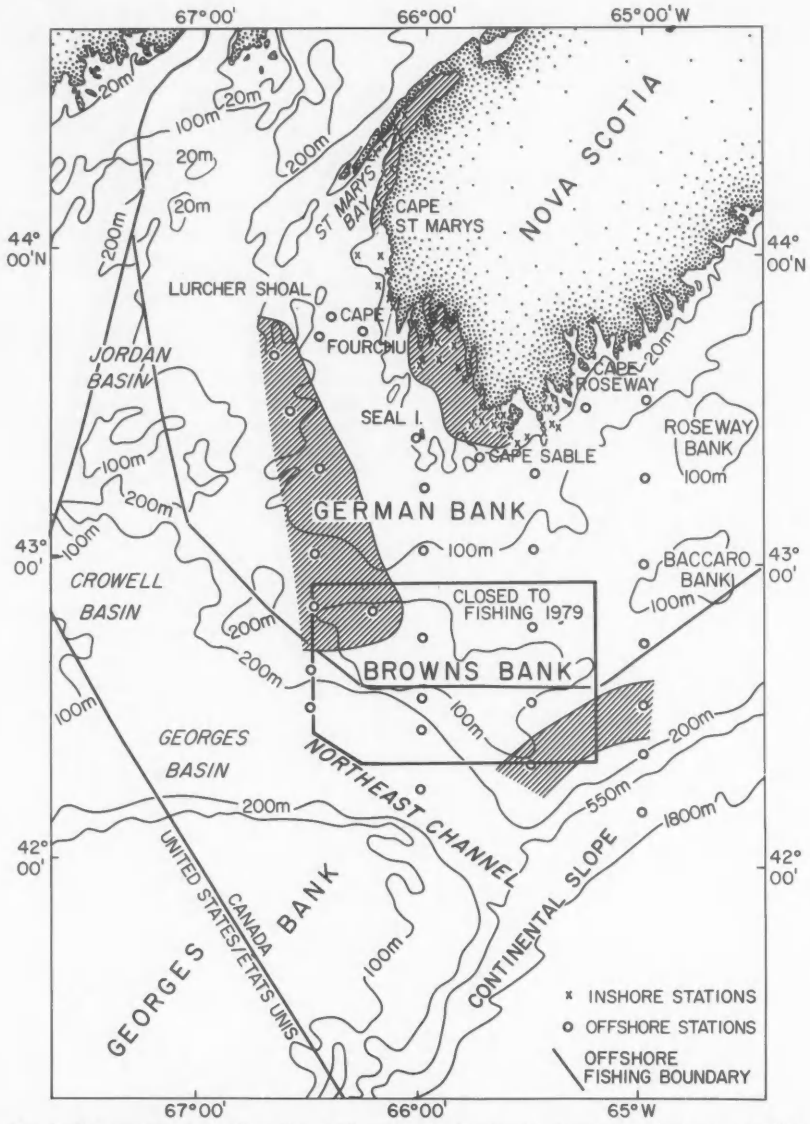

FIG. 1. Bathymetric chart off southwest Nova Scotia showing the locations of inshore and offshore sampling according to Stasko and Gordon (1983), offshore fishing boundary according to existing management (1971–?), Browns Bank closure area (1979–?), and Canada–USA boundary. Regions with important releases of stage I larvae in 1977 and 1978 are hatched (see text).

during the closed season for inshore regions. Values range from 0.7 to 4.3% for eggs about to hatch in July to 6.9–9.4% for recently extruded eggs in September. Pezzack (1983) found with experimental trapping surveys over much of the areas we denote as offshore (German and Browns Banks) that 69, 13, and 67% of the female lobsters were egg bearing in September/October 1980, July 1981, and October 1981, respectively. In the August to September period when lobsters are expected to be in shallower waters, Duggan and Pezzack (1985) found that between 6.9 and 14.6% of the female population were egg bearing on southwest Browns Bank and 21.6 to 29.5% on southeast Browns Bank between 1977 and 1983.

D. S. Pezzack provided us with the size-frequency data for males, females, and egg bearing female lobsters of inshore and offshore regions off southwestern Nova Scotia, as depicted in figures 2 and 4 (of Campbell and Pezzack (1986)). If we use population estimates of ~5200 t inshore and ~1500 t offshore (the latter being highly subjective, see above) and assume that 2.6 and 8.1% of the total population by weight are egg bearing inshore and offshore, respectively, together with the corresponding berried female size-frequencies (from Campbell and Pezzack 1986), we calculate with the fecundity versus body size function for the region (Campbell and Robinson 1983) that an average of $\sim 3 \times 10^9$ eggs·yr^{-1} would have been produced in

both regions in 1977 and 1978. Clearly estimates of this sort are only crude indications of larval production until we have less subjective estimates of the offshore population size and more precise information on the percentage and size-frequency of egg bearing females in all regions.

Larval Production from Plankton Surveys

Larval production estimates for inshore and offshore regions were calculated (Harding and Trites 1988) from the combined 1977 and 1978 larval lobster abundance summaries given in table 2b in Stasko and Gordon (1983). Certainly, it would have been better to use the measured abundance at each sampling site but this information was not given. Each station was sampled with two gear types at three different near surface depths (Stasko and Gordon 1983). Therefore, the abundance data of lobster larvae collected by different shaped nets was converted from a volume to an area basis to obtain an estimate of the number of larvae per square kilometre during each sampling period. Production was then calculated for each of the five sampling periods chosen by Stasko and Gordon (1983), correcting for temperature dependent stage duration and days between sampling after Scarratt (1964) as is standard practice (Scarratt 1973; Harding et al. 1979, 1982; Bibb et al. 1983; Fogarty et al. 1983; Hudon et al. 1986; Harding and Trites 1988). Average sea surface temperatures for the region (Colton and Stoddard 1972; Dobson and Petrie 1983, 1984, 1985), together with laboratory-derived larval development rates (Templemen 1936; Mackenzie 1988), were used for field stage duration determinations.

Pezzack correctly suggests that for a more meaningful interpretation we should have given some estimate of the variance around our calculations of inshore and offshore production (Harding and Trites 1988). Initially we did not examine the variability in the larval lobster surveys because the larval abundance per unit volume was not given in the original report and inshore results were grouped into five regions and averaged (see Stasko and Gordon 1983). However, information on the number of larvae per gear type, standardly towed over 30 min at 2 $m \cdot s^{-1}$, at the time of each sampling (see appendix II in Stasko and Gordon 1983) does enable us to calculate larval variability for the offshore surveys. The calculated abundance-frequency distributions of stage I and IV lobster larvae per station per sampling, for both years combined, are highly skewed with a long tail due to both the preponderance of stations with no lobsters and the occasional aggregation of larvae. Both stage I and IV distributions can be fitted to a negative binomial (χ^2; $P>0.5$) with k values for individual sampling periods ranging from 0.08 to 0.12 for stage I lobster and from 0.18 to 0.90 for stage IV lobster. Ideally one would fit the data to a frequency distribution using general linear modelling techniques (McCullagh and Nelder 1983); however, for the present purposes we used the log $(x+1)$ transform for calculating confidence intervals for a negative binomial distribution with zero values (see Elliot 1977). We applied the percent variability calculated for offshore production to inshore production as well although this is an obvious overestimate. Between 3.0×10^6 and 1.2×10^7 stage I lobster (95% confidence interval) were produced inshore ($\bar{x}=3.7\times10^6$) compared with 3.4×10^7 to 1.3×10^8 stage I lobster produced offshore ($\bar{x}=3.4\times10^7$) over the 2-yr period. Included in this estimate would be (1) between station, (2) sampling date, and (3) year to year variability, as well as the effect of net clogging (no flow meters were used) and the change in experimental design from around-the-clock sampling in 1977 to daylight sampling in 1978. Vertical migration is certainly responsible for the greater variability and abundance of stage I lobster in 1977 (Harding et al. 1987). The sampling grid was not completed during each survey in 1977, presumably due to bad weather, but the effect on production estimates should be minimal because these incomplete earlier surveys largely preceded larvae lobster release in the area (see Stasko and Gordon 1983). The regular deletion of the five shoreward stations of the offshore grid in 1978 is unfortunate and will have had the effect of raising the offshore estimates because few larvae were released at these sites in the previous year.

Stage IV lobster larvae were probably adequately sampled by Stasko and Gordon (1983) because they inhabit the upper 1-m layer of the ocean both day and night (Harding et al. 1987); however, some of these larvae could have originated from a distant source if they are carried by ocean currents (Harding and Trites 1988). Between 3.1×10^6 and 6.5×10^6 stage IV lobsters (95% C.L.) were produced inshore ($\bar{x}=3.6\times10^6$) compared with 8.6×10^7 to 1.8×10^8 stage IV offshore ($\bar{x}=1.0\times10^8$) over the 2-yr period. Contouring the seasonal abundances of stage IV lobster on the 1977 and 1978 survey grids also indicates that the greatest concentrations of larvae occurred around German and Browns Bank.

Concluding Remarks

It appears that there are substantially more lobster larvae produced offshore than inshore (by our definition) off southwestern Nova Scotia. At present it is impossible to know whether the more numerous offshore larvae have an equal chance of survival compared with those inshore. There is some cause for optimism in this regard in that several investigators have analysed independently the 15 yr time series of larval lobster production in Northumberland Strait (Scarratt 1964, 1973) for predictive purposes using either estimated stock size or commercial landings and obtained significant correlations which explained between 36 and 77% of the variation (Scarratt 1973; Robinson 1979; Harding et al. 1982; Fogarty 1983). We concur, however, with D. S. Pezzack that a stock–recruitment relationship such as this can not account for the recent rise in lobster landings throughout the Maritimes in the 1980's. These pulses in recruitment have occurred before in the early 1930's and mid 1950's and may represent an environmentally determined response of the population.

We obviously have a lot more to learn about the relationship between inshore and offshore lobsters around the Gulf of Maine. The results of the larval lobster survey conducted from St. Andrews, reanalyzed here, has led us to believe that a separation exists between inshore and offshore larval release sites off southwestern Nova Scotia, although this may not be the case further into the Gulf of Maine. A new study, incorporating our improved understanding of the daily vertical movements of larval lobsters, is needed to confirm and refine these findings. It is equally important to obtain better information on the abundance and whereabouts of egg bearing females between June and early September, in both the inshore (<20m) and offshore along the 100-m isobath between Browns Bank and Lurcher Shoal. These approaches will give us a better understanding of inshore and offshore recruitment to the region though it will not resolve whether inshore lobsters are derived partially or largely from offshore larvae. A refinement of our understanding of the physical environment and processes in the area would

improve the larval dispersion hypothesis we developed (Harding and Trites 1988). A more positive proof of inshore–offshore lobster continuity or discreteness could come from protecting marked inshore lobster as they recruit into the inshore fishery which would enable later recognition if they do gradually move towards greater depths with age.

Our original intent in Harding and Trites (1988) was to explore the role of advection and dispersion of larval lobsters in the Gulf of Maine. Our conclusion stands that larvae are transported from Browns Bank towards inshore areas and could be significant to inshore recruitment — G. C. Harding and R. W. Trites, *Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2.*

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ANNOUNCEMENT/AVIS

The Fisheries Society of the British Isles International Symposium on The Biology and Conservation of Rare Fish

International Symposium on the Biology and Conservation of Rare Fish; University of Lancaster, England, 16–20 July 1990. The symposium will review the problems of fish conservation globally, describe research and action in progress and needed for the future. It will include topics such as: threats to fish from fishing, introductions of aliens, habitat degradation; the present status of rare fish globally; population-dynamics and ecology, conservation of sub-specific taxa and stocks, genetic conservation; methods of managing fish conservation, habitat improvement, breeding and restocking, laws. Full details from: Dr T. B. Bagenal, Tarnside, Lupton, Kirkby Lonsdale, Carnforth, LA6 2PP, England.

(La Société des pêches des Isles britanniques) Symposium international sur la biologie et la conservation des poissons rares

Symposium international sur la biologie et la conservation des poissons rares. Université de Lancaster, Angleterre, 16 au 20 juillet 1990. Le symposium traitera des problèmes de la conservation, à l'échelle mondiale, des espèces de poisson ainsi que des recherches et mesures qui sont ou devront être réalisées ou prises. Les travaux seront axés sur les domaines suivants: les menaces liées à la pêche, à l'introduction d'espèces étrangères et à la dégradation des habitats; la situation actuelle des espèces rares au niveau mondial; la dynamique des populations et l'écologie, la conservation des stocks et des taxons infraspécifiques, la conservation des caractères génétiques; les méthodes de la gestion en vue de la conservation, l'amélioration des habitats, la reproduction et l'ensemencement, et la législation. Des renseignements détaillés peuvent être obtenus en s'adressant à: Dr. T. B. Bagenal, Tarnside, Lupton, Kirkby Lonsdale, Carnforth, LA6 2PP, England.

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